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The Morphology of Araucaria brasiliensis — L. Lancelot Burlingame

The Climax Forest of Isle Royale, Lake Superior, and Its Development. II — William S. Cooper

Macrozamia Moorei, a Connecting Link between Living and Fossil Cycads — Charles J. Chamberlain

A Protocorm of Ophioglossum — Loren C. Petry

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THE MORPHOLOGY OF ARAUCARIA BRASILIENSIS (WITH ELEVEN FIGURES AND PLATES IV AND V). *L. Lancelot Burlingame* - - -

VOLUME LV NUMBER 2

THE
BOTANICAL GAZETTE

FEBRUARY 1913

THE MORPHOLOGY OF ARAUCARIA BRASILIENSIS

I. THE STAMINATE CONE AND MALE GAMETOPHYTE

L. LANCELOT BURLINGAME

(WITH ELEVEN FIGURES AND PLATES IV AND V)

Introduction

Although wood of the araucarian type, strikingly resembling that of the ancient Cordaitales, has been known for a long time and has been used as evidence of the antiquity of the araucarians and as a proof of their relationship to the Cordaitales, both of these opinions have been vigorously challenged. It has been asserted that they are less ancient than the Abietineae and are derived from them (**7, 9**); that possibly they are not related to other gymnosperms at all and have been derived from a lycopod ancestry (**17, 18, 20**); that "the geological claim for the great antiquity of the Abietineae thus fails on critical study of the two forms upon which it is based" (**27**); that "the ancient geological and widely separated geographical distribution (of Araucarineae), the large microsporangiate cones in comparison with the megasporangiate cones, the evident transition between the sporophylls and the foliage leaves are indications of an interesting and probably primitive group. The anatomy of the microsporophylls and megasporophylls indicates that they are homologous structures, functionally differentiated" (**26**); that "unfortunately, no teratological phenomena, on which he always laid great stress, were known in the *Araucariae*, but they were in the Abietineae and showed that

the single ovule was a modification of an axillary shoot bearing sporangia" (**30, 31**).

In the face of opinions so diverse, the desirability of additional facts is very evident. We know already that the pollen grains and pollen tubes of *Araucaria* contain numerous nuclei, most of which are prothallial or vegetative (**13, 24, 25, 26**), and that the same condition obtains in *Agathis* (**24**), with the added information that there are definitely "two large male nuclei" (**6**). Among the Podocarpineae the same conditions are known to be true for *Podocarpus* (**1, 2, 5, 8, 22, 33**), *Dacrydium* (**8, 23, 32, 33**), *Phyllocladus* (**11, 33**), *Saxegothaea* (**15, 29**), and *Microcachrys* (**28**). The present investigation was undertaken in the belief that additional knowledge of the morphology of the Araucarineae would aid very materially in clarifying our ideas concerning the origin (or origins) of Coniferales and the relationship of the Pinaceae, particularly the Abietineae, and the Podocarpineae (and Taxaceae generally).

The materials for this investigation have been secured through the kindness of Mr. JAMES C. FLOOD of San Francisco, California, from his country place, Linden Towers, at Menlo Park, California, to whom the writer wishes to express his sense of obligation and appreciation. He is also under obligation for actual assistance in making the collections to the generous assistance of Mr. ROACH, the gardener at Linden Towers, to whom also his thanks are due. Collections were begun in March 1910 and made weekly up to the middle of November, when they were interrupted by illness until February 1911. Collections were again made from November 15, 1911, to February 1912, thus completing the series.

Various killing and fixing agents have been tried. A solution recommended by JUEL (**10**) gave as satisfactory results as any for most stages. Flemming's stronger solution, as well as the chrom-acetic mixture recommended in CHAMBERLAIN'S *Methods in plant histology*, also gave good results for some stages, but fails to penetrate the microsporangium during the development and division of the mother cells, owing partly to the nearly impervious epidermis that develops about this time, and partly, perhaps, to the presence then in the pollen sacs of a sort of mucilage, apparently produced by the

degeneration of the walls of the mother cells. At certain times in mid-winter practically all stages of the cones are present on the trees at the same time. Notwithstanding the fact just mentioned, stages between the prophase of the mother cell and tetrads were collected only four times, though diligently sought for. The same is true of the stages in the development of the gametophyte from mature microspores to those in which the primary spermatogenous

FIG. 1.—Forest of *Araucaria brasiliensis* on the Rio Tibagy, State of Parana, southern Brazil.—Photograph by J. C. BRANNER.

cell has already divided. The reasons for this state of affairs are not very apparent, though it may be that these stages are passed through very rapidly or that division occurs during the night.

The habit of the tree is shown in text fig. 1, representing old trees in their native habitat, and in text fig. 2, an ovulate tree from the gardens at Linden Towers.

The staminate cone

Among the numerous specimens of *Araucaria* in these gardens, belonging to at least four different species, there are three staminate

ones of *A. brasiliensis*. They are about 30 years old and range in height from 25 feet to about 60 feet. The largest one is about 20 inches in diameter. Most of the collections were made from the smallest tree because it has had the crown broken out, and on this account fruits much nearer the ground, a matter of some

FIG. 2.—Ovulate tree from gardens at Linden Towers, showing retention of lower branches in young trees.

consequence when one considers ways and means of securing cones from a "monkey puzzle" tree. This tree was selected for the additional reason that the range of stages on it at any time was greater. It had moreover the peculiarity of forming its cones much earlier in the fall and continuing to form new ones later in the

spring. Numerous collections were made from one of the other trees in order to make sure that development in the cones from all the trees was the same.

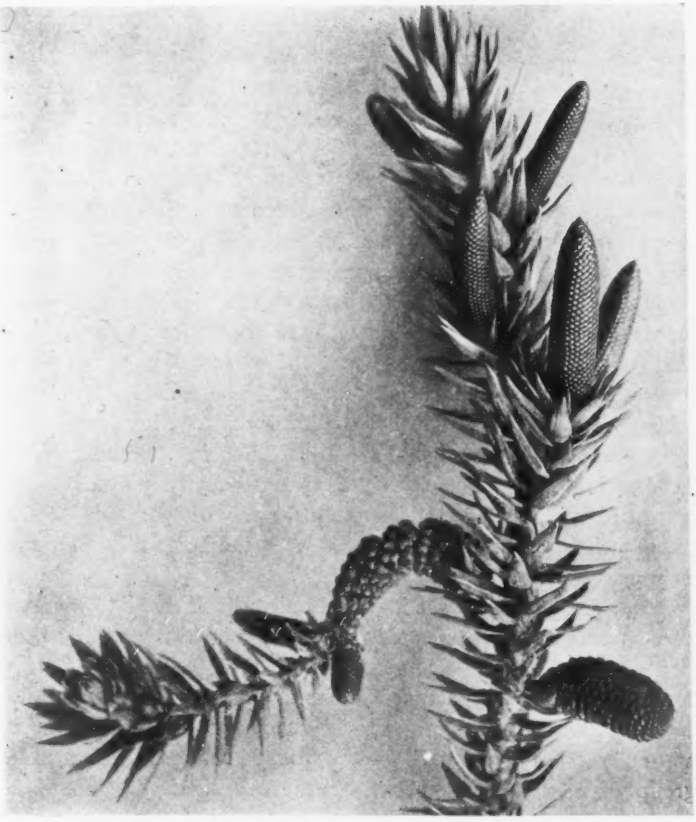


FIG. 3.—Staminate branch of *A. brasiliensis* bearing two old cones of previous season and several young ones; note the new shoot from one of the old cones.

In the fall (August to October) one finds the shoots of *A. brasiliensis* tipped with terminal buds, in some of which, distinguished by being larger and plumper, one can find the very young cones. As soon as the branch has developed from such a bud, one

usually finds about 3–6 staminate cones scattered along the new shoot (text fig. 3). Each cone terminates a short leafy branch, which may occasionally continue its growth the following season, but usually the cone dries up, turns brown, and falls off the winter following the shedding of its pollen (text fig. 3). The mature cones are very large, immediately after having shed their pollen being frequently as much as 15 cm. long and 3 cm. in diameter; they are about one-third smaller before shedding. Text fig. 4 shows an unopened cone, a cone shedding its pollen, and the apical view of a mature cone broken in two, about natural size. Such a cone as is shown in the photograph has about 1000 sporophylls, disposed in about 12 spiral rows, each of which makes 2 or 2.5 turns. There are usually 10–15 sporangia, pendent (text figs. 5 and 6) from the expanded distal portion of the sporophyll on its morphologically abaxial side. Each sporangium contains 500–1000 pollen grains. A little calculation will show that the output of a terminal bud may easily reach a billion pollen grains. The pollen is shed in the spring from the first of April to the latter part of May for the most part, although I have found cones shedding in December and as late as July 1. The sporangia dehisce through longitudinal slits on the sides of the sacs facing the other row of sporangia, so that the pollen is shed into the space between the inner and outer rows of sporangia.

By dissecting the terminal buds already referred to, one can recognize the young cones when they are merely rounded growing points. Each one is enveloped in two or three layers of delicate leaves and is slightly flattened on the side next the main axis of the bud. Plate fig. 1 shows a slightly older cone, on which the first sporophylls are forming. A sporophyll is first recognizable as a group of meristematic cells (plate fig. 2) just beneath a slight emergence of the smooth surface of the growing point (plate fig. 1). This emergence increases in size rapidly by growth throughout. Very soon its distal end expands until the whole structure somewhat resembles a mushroom with a very short stalk and one-half of the pileus removed. The stalk is so short that the abaxially placed swollen portion of the sporophyll is in contact with the cone axis. From its surface grow the sporangia, elongating toward the cone

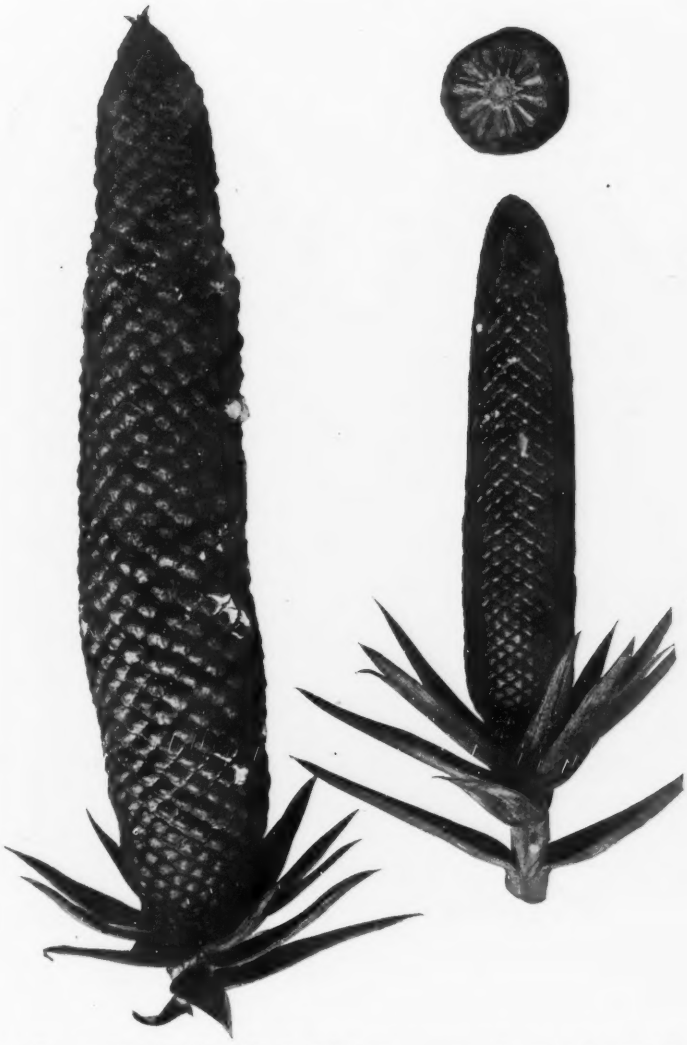
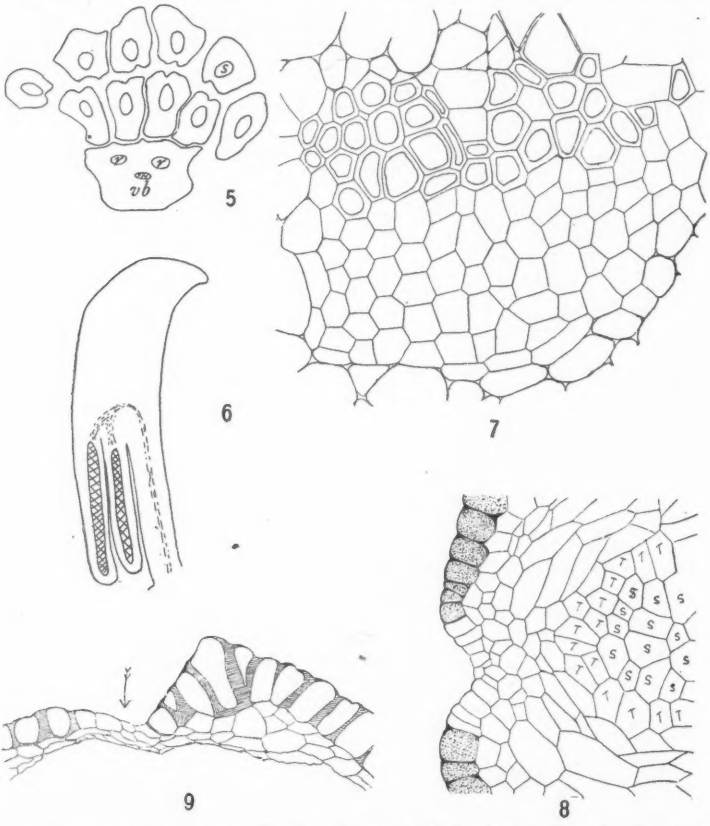


FIG. 4.—Cone shedding pollen (to right), mature unopened cone, and cross-section of mature cone; natural size.

axis as fast as the axis of the sporophyll itself elongates. Like the sporophyll itself, the sporangia are first distinguishable as meri-



FIGS. 5–9.—Fig. 5, cross-section of sporophyll, showing relation of sporangia to one another and to the stalk; fig. 6, longitudinal section of a sporophyll, showing position of sporangia and course of their vascular supply; fig. 7, cross-section of a vascular bundle of sporophyll; fig. 8, cross-section of a sporangium at mother cell stage, showing sporogenous cells (*s*), tapetal cells (*t*), 4–6 layers of wall cells, tannin-filled epidermal cells, and thin cells where dehiscence will take place; ×250.; fig. 9, annulus and stomium just before dehiscence; ×250.

stematic outgrowths consisting of several cells. Plate fig. 3 shows part of three sporangia adjacent to one another in the same row, and plate fig. 4 shows a section at right angles to it, showing the

beginnings of two sporangia adjacent to one another but in different rows.

Occasionally one can distinguish what appears to be the archesporium almost as soon as the sporangium itself is recognizable, but much more commonly it cannot be detected until the sporangium is 12–15 cells in length and 8–10 cells wide (plate figs. 4, 5, 6). Not infrequently sporangia as far developed as that shown in plate fig. 7 do not show any differentiation of sporogenous cells. Ordinarily one can recognize all the primary regions of the sporangium at this stage. The cells of the tapetum seem to be derived more or less indifferently from those of the wall layers outside, or from derivatives of the inner and presumably sporogenous cells. However, I should not like to be too dogmatic in regard to this. Multiplication of cells continues until the sporogenous tissue consists of a mass some 20 cells in cross-section (plate fig. 8) and 40–50 cells long. The tapetum remains one or two cells thick, the ultimate cells being elongated radially and retaining their position and structure till some time during the development of the male gametophyte. At this time there are 4–6 layers of wall cells radially flattened, with very little cell contents. The epidermis is at this time filled with a densely staining substance, resembling tannin in its staining reactions, and presenting a very effective barrier to the ready penetration of the ordinary reagents. In the further development of the sporangium the contents of these epidermal cells disappear, and the radial walls, seen in a cross-section of a sporangium, thicken in the fashion of a fern annulus, except at the point of future dehiscence. The wall cells are eventually crushed and more or less destroyed and the tapetum finally disintegrates (text figs. 8 and 9).

Sporogenesis

After the last division of the sporogenous cells, the mother cells begin enlarging, until at the prophase of the heterotypic division they have attained a diameter more than twice that of the sporogenous cells. This eight or ten times increase of volume is largely water, the cytoplasm becoming greatly vacuolated as the growth increases. There is a corresponding enlargement of the nucleus,

though not proportionally so great (plate fig. 9). Once this increase in size has been effected in the mother cells and their walls, the cell contents appear to round up and shrink away from the walls more or less; just how much I am unable to say owing to the difficulty of determining whether part or all of the shrinkage may not be due to the difficulties of securing satisfactory fixation. The walls themselves have a tendency to persist until after the young spores have been formed, but apparently they change their chemical condition and become more or less mucilaginous in character. Sometimes no walls at all are visible, but the spaces among the mother cells are filled with a thin sort of mucilage. The greater the amount of this mucilage present, the poorer the fixation.

Owing to the difficulties already mentioned, I have but little trustworthy information concerning the course of events during the reduction divisions. Stages in the formation of the presynaptic spireme, synapsis, and diakinesis were observed. At the metaphase of the heterotypic division there are 8 bivalent chromosomes, but the material did not permit one to follow the method of their formation. The spindle fibers are attached to their apices (plate fig. 11), and they are drawn apart as short stubby masses and collect at the pole in a close mass. They appear at the spindle of the homeotypic division as much longer rods curved into more or less U-shaped chromosomes. No walls are formed, apparently, until after the spore nuclei have passed into the resting condition, when a system of fibers is present between the nuclei, on which the plasmatic membranes separating the young spores arise (plate figs. 13 and 14).

The young spores now form walls around themselves, entirely within the old mother cell wall if it is still present. The spores then begin a slow enlargement and thickening of the walls. At first the growth consists merely in enlargement of the wall without any apparent increase of cytoplasm or nucleus. There is either one very large vacuole almost entirely filling the spore or many smaller ones separated by only the most tenuous cytoplasmic walls. At this time no inclusions of starch or other food materials are visible. After the spore wall has reached its mature size, but not final thickness, the cytoplasm becomes more abundant and the nucleus enlarges (plate figs. 16 and 17). In the large nucleus there is a large

nucleolus and rather scanty chromatin. From this is organized a rather long, loose spireme, apparently containing scanty chromatin. It segments to form 8 chromosomes, which contract into rather small dense oval masses (plate fig. 18).

Male gametophyte

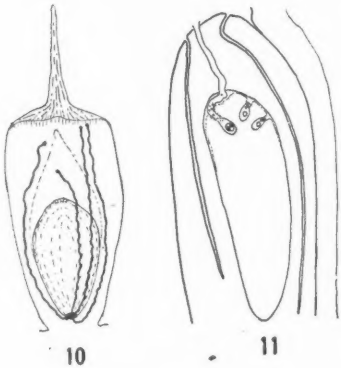
The results of this first division are a primary prothallial cell and a free nucleus (plate fig. 19). The latter at once divides to produce a second prothallial cell, which takes its place over the preceding. The next division yields the free tube nucleus and the primary spermatogenous cell (plate fig. 21). Meantime the prothallial cells have divided (plate figs. 20, 21, 22). The primary spermatogenous cell now divides, yielding the usual stalk and body cell. The stalk cell is very evanescent, usually becoming confused with the general cytoplasm very quickly. Plate fig. 25 shows one of the few preparations in which it could still be distinguished as a distinct cell. Another interesting case was observed in which there seemed to be two free and equal cells in the unshed pollen grain. The usual condition of a mature pollen grain, with 15–25 free prothallial nuclei, a recognizable tube nucleus, and a single body cell, is shown in plate fig. 27.

It is in this condition that the pollen is shed in April (usually). The potential number of pollen grains is four to eight times as great as the actual number formed. It has already been remarked that the ordinary number of mother cells is about 1000, while the usual number of pollen grains that mature in a sporangium is only 500–1000. At the time they are shed the pollen grains have a two-layered wall, the outer coat of which easily separates from the inner (plate figs. 25, 26, 27), but which does not appear to do so naturally to form wings. At the time they are shed they contain a great many very large starch grains, a few of which are shown in plate fig. 27. They are usually so crowded with it that the microtome knife scatters the contents all about in cutting sections of shed pollen.

Pollination

The ovulate cones are first recognizable in late April. At this time there is no trace of ovules on the scales and the pollen lodges somewhere near the free edge of the so-called ligule (text fig. 10).

Whether the pollen shed in the early part of the season finds a lodgment in a position to become effective is uncertain. Neither does there appear to be any available data as to whether this precocious shedding of pollen occurs in its native habitat. Though California and Brazil exhibit a somewhat rough correspondence in their seasons of rainfall and plant growth, yet it is probably not sufficiently exact to permit of any very satisfactory inferences as to the corresponding behavior in the two habitats.



FIGS. 10, 11—Fig. 10, ovule and scale in December, showing course of pollen tubes; fig. 11, course of pollen tube through nucellus to archegonium.

I have not yet ascertained certainly how long a time elapses after the pollen falls on the scale before germination occurs. Grains that have germinated can be found in the latter part of summer after the fogs have set in. Meantime during the summer the ovule is forming and the stigmatic nucellus is usually ready to receive the advancing pollen tubes some time in September or October.

I have not so far succeeded in germinating pollen to any very advanced stage, nor have I been able to follow with any certainty the course of events in the pollen tube before it reaches the nucellus. When the ovuliferous scales are pulled apart, very numerous pollen tubes are usually found sewed back and forth between the two adjacent surfaces of the scales. One can sometimes isolate one without completely destroying it, but I have learned from such preparations nothing more than that there are numerous nuclei and a body cell present. One could infer that they would be there, inasmuch as they were in the pollen grain, and they are afterward present in the tube when it enters the nucellus. Whether division of the prothallial nuclei occurs in the tube or not is uncertain, owing to the fact that I have never been able to obtain an entire tube in which I

could count the nuclei and be sure of having seen them all. These nuclei do increase markedly in size, and much of the starch which entered the tube at germination disappears before penetration of the tube into the nucellus.

At the time that the tube enters the nucellus there are numerous nuclei and the body cell present. I was unable to distinguish the tube nucleus any longer from the others. At first only a few of these nuclei enter the portion of the tube in the nucellus. The body cell is usually in that portion just outside of the nucellus or just barely within it. There is apparently very little activity in the development of the tube from the time it first penetrates the nucellus for a short distance until spring. I did not succeed in finding the mitosis concerned in the division of the body cell, though the two male cells were found two or three times still imbedded in a common mass of dense cytoplasm. The two nuclei frequently differ in size markedly. The body cell and its nucleus have increased in volume after leaving the pollen grain some six or eight times by the time the pollen tube has penetrated the nucellus in October (plate fig. 28). This increase continues on an even greater scale up to the time of division. After the division of the body cell, one, at least, of the pieces organizes itself into a large male cell or perhaps a real sperm. These vary considerably in size and in the definiteness of their organization. They all agree in being very large and in being more or less completely delimited from the cytoplasm in which they are imbedded (plate fig. 29). Almost invariably the large nucleus is at the extreme end of the cytoplasm and the cytoplasm is very often evidently arranged in such a way as to lead one to surmise that the nucleus actively changes its position in reference to the cytoplasm. The nucleus is invariably at that extremity which would lead in the direction that the "sperm" would be inferred to be moving. The cytoplasmic body is sometimes bent, almost at a right angle in one instance observed, in such a way as to remind one strongly of the creeping movements of an amoeba. In one instance of two "sperms" lying in a common mass of cytoplasm, apparently having just divided, there was present a peculiar fibrillar structure reminding one of a nuclear spindle without the chromosomes and with an aster at either pole. Whether this is

an indication of the presence of a blepharoplast and whether the "sperm" is actually motile, I hope to be able to ascertain during the coming spring. The division probably occurs in the latter part of February and in the part of the tube outside of the nucellus.

During this time the pollen tube has advanced through the nucellar tissues in a more or less irregular and branching course. When it reaches the upper part of the female gametophyte it usually turns aside from the apex, which is protected by a cap of crushed nucellar cells, and creeps laterally along the surface of the gametophyte until it reaches the narrow opening leading down to one of the archegonia, down which it descends to the neck of the archegonium. Here it becomes perforated. The "sperm" passes through the opening and crowds the neck cells of the archegonium apart without destroying them, and plunges down into the egg so vigorously as to leave a very distinct wake behind it in the cytoplasm. Fertilization occurs in the latter part of March or first week or two of April.

Discussion

It is not proposed at this time to enter into any general discussion regarding the broader questions that prompted the investigation, but to let that await the issue of further investigation of other phases of the life history of this species and of the other three species of which material is available. However, it may not be amiss to point out that this added information concerning the male gametophyte goes far toward inducing a belief in the primitive condition of the araucarians. It certainly strengthens the resemblance to the podocarps and tends to increase our confidence in their genetic connection. Barring the abnormally large "sperms" of *Araucaria* and the greater number of prothallial nuclei, its male gametophyte exhibits an almost identical structure even in small details with that of the Podocarpineae. On the contrary, it is clear that the type of male gametophyte found in these two tribes is essentially different from that found in *Cupressus Goveniana* (**10**) and *Juniperus communis* (**14**). In these we have a multiplication of spermatogenous cells, which may be induced, as has been suggested, by the opportunity for more than one sperm to function, but in any case is doubtless a reversion to an ancient habit (**10, 14**). This view

is strengthened by the occurrence of more than two sperms in *Microcycas* (**3**) and *Ceratozamia* (**4**). The deposition of the pollen at a distance from the nucellus has also been recorded for *Saxegothaea conspicua* (**15**), and serves to strengthen the likeness of the araucarians and podocarps.

By long odds the most interesting and suggestive feature of the male gametophyte of the araucarians yet known is the remarkably large "sperms" and the possibility of their motility. The one figured (plate fig. 29) is about 150 μ long. It is by no means the largest one observed, but seemed to be the one most definitely organized. Such dimensions are only known elsewhere among the actively swimming sperms of the Cycadales and *Gingko*. It is of interest to note that the kauri (**6**) appears to have two large nuclei also, though it is not stated that they constitute part of organized cells. Inasmuch as *Agathis* has usually been held to be more primitive in most respects than *Araucaria*, it may be possible that they will yet be found there. The aster-like fibers found in the dividing body cell are of course very suggestive of a blepharoplast, and one might perhaps legitimately expect such structures to be found in connection with such large and possibly motile male cells. Again they might be only such structures as have been recorded by LAND (**12**) in the egg of *Ephedra*.

Summary

1. The staminate cones are extraordinarily large and have numerous sporophylls with an indefinite number of pollen sacs pendent from the abaxial side of the swollen apex.

2. An almost incomprehensibly great number of pollen grains is produced.

3. The method of differentiating the sporogenous tissue is variable and indefinite. The size of the sporangium and the number of microspores is subject to wide fluctuations.

4. The structures concerned in dehiscence are very fernlike.

5. The chromosome number in the male gametophyte is 8.

6. Prothallial tissue is formed in a manner almost identical with that in the Podocarpineae, but the number of cells so formed is greater.

7. The pollen is shed with numerous prothallial nuclei, stalk nucleus, tube nucleus, and body cell free in it.

8. The pollen does not fall upon the nucellus but upon the ovuliferous scale at a considerable distance from the position of the ovule.

9. About a year elapses between pollination and fertilization.

10. No ovule has yet been formed on the scale at the time of pollination and the pollen tube does not reach the ovule for 5 or 6 months afterward.

11. The body cell is single, at least usually, and large.

12. Two male cells (sperms perhaps) are formed and are usually unequal.

13. There may be a blepharoplast-like body associated with the division of the body cell.

14. Fertilization occurs about the first of April.

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EXPLANATION OF PLATES IV AND V

All figures have been drawn under Zeiss apochromatic objectives and compensating oculars with the aid of a camera lucida. Figs. 2–8 were drawn with 4 mm. obj. and compensating ocular 6; figs. 9–27, under obj. 3 mm. and ocular 12; figs. 28 and 29, under 3 mm. obj. and compensating ocular 6.

Fig. 1.—Longitudinal section of a young cone from a terminal bud: *sc*, scale leaf; *sp*, young sporophyll; *vb*, vascular bundle; ×12.

Fig. 2.—Primordial meristem of very young sporophyll drawn from same cone as fig. 1; ×250.

Fig. 3.—Cross-section of a cone showing the sporangial meristems; ×250.

Fig. 4.—Longitudinal section of cone of same age as preceding: section passes through the stalk of the sporophyll and through the primordia of one sporangium in each row; *c.ax*, axis of cone; ×250.

Fig. 5.—Transverse section of cone and longitudinal section of sporangium: sporogenous tissue not defined; ×250.

Fig. 6.—Same as fig. 5, but showing usual differentiation of sporogenous tissue (*spt*); ×250.

Fig. 7.—Usual stage of differentiation of tapetum (*t*); ×250.

Fig. 8.—Cross-section of sporangium after last sporogenous division; ×250.

Fig. 9.—Somewhat shrunken mother cell showing eight times increase in volume; ×770.

Fig. 10.—Portion of a nucleus in which the heterotypic chromosomes are forming; ×770.

Fig. 11.—The 8 heterotypic chromosomes; ×770.

Fig. 12.—Second division of mother cell; ×770.

Figs. 13 and 14.—Tetrads, showing cell division; ×770.

Fig. 15.—A group of young microspores; ×770.

Figs. 16 and 17.—Mature microspores; ×770.

Fig. 18.—Division of microspore nucleus; ×770.

Fig. 19.—Showing first prothallial cell (*pc'*); ×770.

Fig. 20.—Mitosis of a prothallial cell; ×770.

Fig. 21.—Showing two tiers of prothallial cells (*pc' pc''*), primary spermatogenous cell (*p.s.c.*), and tube nucleus (*t*); ×770.

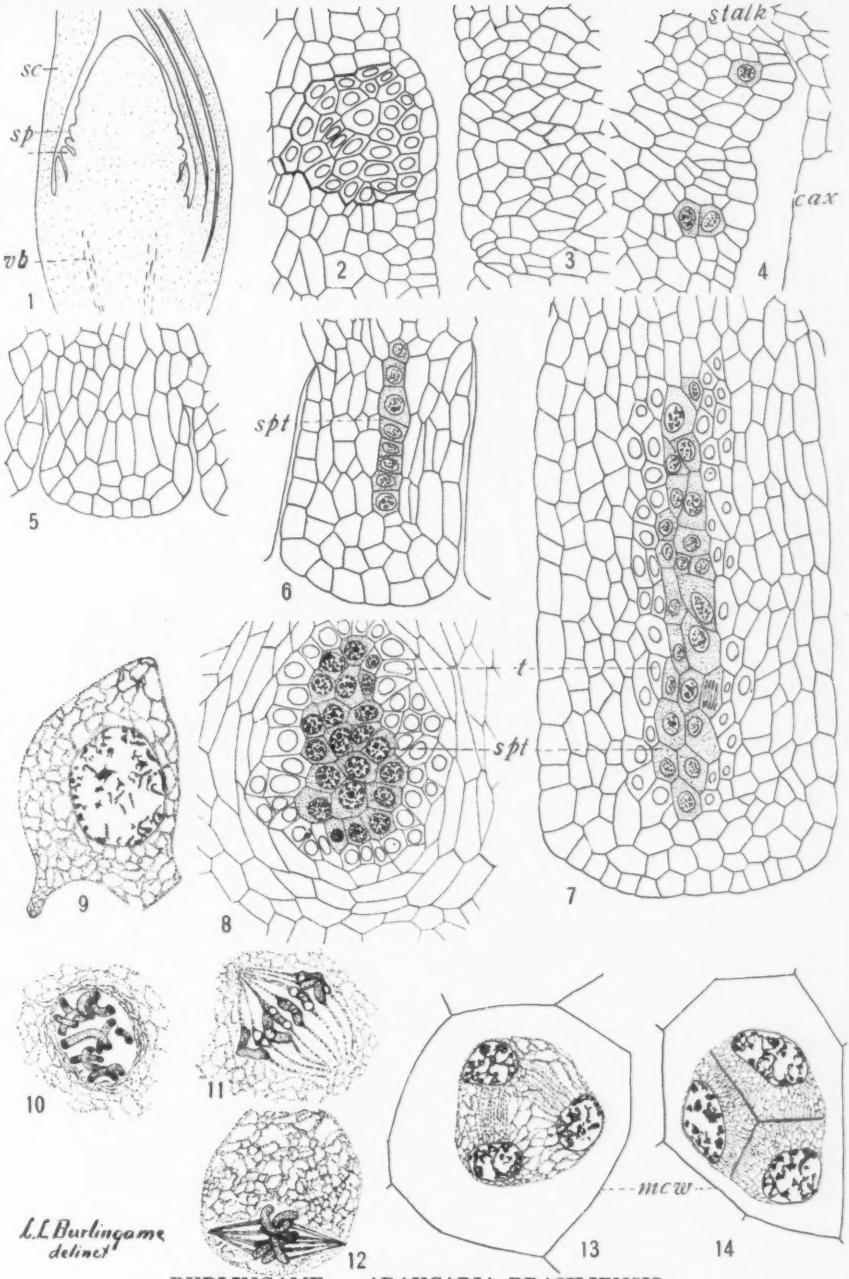
Fig. 22.—Division of primary spermatogenous cell; ×770.

Figs. 23–26.—Series of transverse sections of a pollen grain: *pc'*, basal tier of prothallial cells; *pc''*, second tier; *tn*, tube nucleus; *bcn*, body cell nucleus; *bc*, body cell; *sc*, stalk cell; *scn*, stalk cell nucleus; ×770.

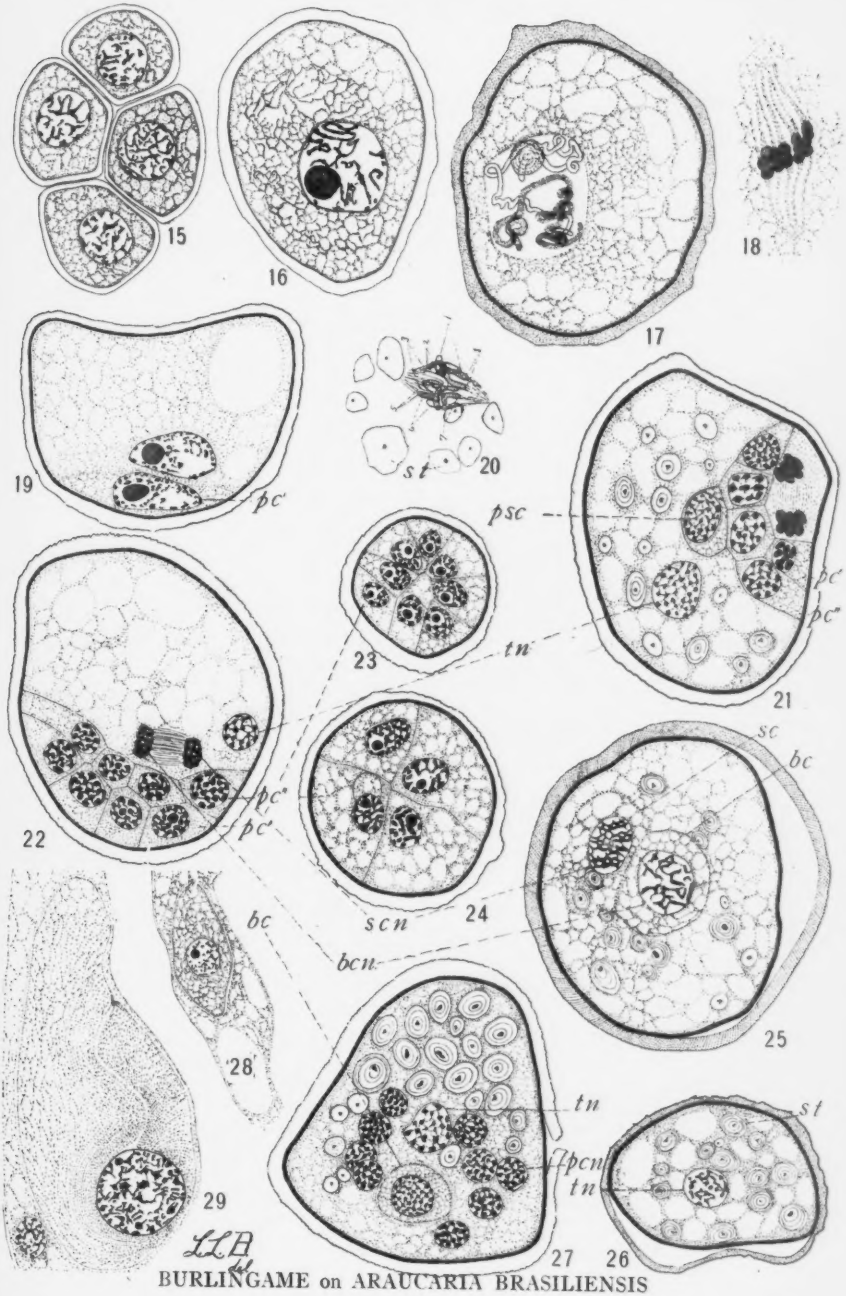
Fig. 27.—Shedding stage of pollen grain; ×770.

Fig. 28.—Body cell about October 15; ×385.

Fig. 29.—A male cell just before fertilization; ×385.



BURLINGAME on ARAUCARIA BRASILIENSIS



BURLINGAME on ARAUCARIA BRASILIENSIS

THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. II

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH SIXTEEN FIGURES)

Part II.—The successions

THE PRIMARY SUCCESSIONS

The xerarch successions

I. Physiographic development of the habitats and description of present shores

The physiographic development of the shore habitats is in large part that of the island itself, which has been briefly outlined in the introduction. Since the postglacial history of Isle Royale has been one of gradual emergence from the waters of Lake Duluth and its successors, it follows that all parts of the island have at some stage of the process been shore.

The present shores of Isle Royale may be classified in several ways. First, there are the rock shores and the beaches, of which the former are vastly the more important. The rock shores may be classified in three ways: according to degree of slope, degree of shelter, and kind of rock involved. According to slope we find two classes: cliff shores and gently sloping shores. These two types are usually sharply distinguished. The cliffs are characteristic of the northwest coast of the island and of its surrounding islets, being produced by the broken edges of the lava and sedimentary layers; while on the southeast coast, the slope of the shores corresponds rather closely with the dip of the rocks, which is nearly everywhere gentle, averaging perhaps 10–15°. The cliffs range from 1 to 20 m. or more in height, are frequently perpendicular, and may sometimes be seen to descend without a break to considerable depths below the surface of the water. According to degree of exposure the shores, both cliff and sloping, may be divided

into those exposed to the lake winds and waves, and those protected from them. In classifying according to kind of rock, the physical, not the chemical, characteristics are the important ones. The rocks of Isle Royale are partly volcanics, which are resistant, and subordinately sedimentaries (sandstones and conglomerates), which are much less so. On the southeast coast of the island the shores, where of volcanic rock, have smooth sloping surfaces, and where composed of sandstone or conglomerate are often much broken and

FIG. 15.—Outer shore of Long Island, southeast of Siskowit Bay: sandstone beds dipping southeast; a glacial bowlder of granite in the foreground; notable disintegration of the sedimentary rock is exhibited; the forest extends low down because the force of the waves is broken by irregularities of the shore (cf. fig. 27, where the degree of exposure is the same).

very irregular (compare figs. 24 and 15). Striking differences in rate of erosion were noted on the northwest coast. Near Blake Point the great "Greenstone" layer, which forms the backbone of Isle Royale, is at the shore, and forms smooth cliffs which rise direct from the water to a height of 20 m. or more. The stable character of these cliffs is shown by the thick coating of lichens which covers them, the belt of brilliant orange *Placodium* being especially conspicuous. Trees of large size, as well as many smaller

plants, are abundant in the crevices (fig. 16). Very different is the shore just southwest of McCargoe's Cove (Sec. 23, T. 66 N., R. 35 W.). The material here is a sandstone, and the cliff is being rapidly eroded by the waves. Lichens are absent, and the soil and forest growth at the top are being undermined. Several recently overturned trees were seen. On the whole, wave erosion at the present lake level has not yet notably modified the configuration of the coast, so that shore recession need not be reckoned with as an important influence upon the vegetation.

FIG. 16.—Inward-facing cliff of one of the small islands bounding Rock Harbor on the southeast: resistant volcanic rock produces stable cliffs; because of sheltered location the limit of forest extension is near the water's edge, but the trees are confined to ledges and crevices.

II. The rock shore succession

With regard to the comparative areas which have been vegetated through the instrumentality of the various successions, both hydrarch and xerarch, the rock shore succession is by far the most important of all. A conservative estimate would indicate that at least nine-tenths of the forest of Isle Royale has developed along the line of this succession. At the same time it is a comparatively simple one, and will not require extended treatment.

The fundamental fact in the process, throughout the history

of the island, has been the occupation by vegetation of new areas left exposed by the retreating waters. Recession has now ceased, temporarily at least, and no fresh surfaces have been presented for a long period of time. The forest in its advance has for this reason in some places practically reached the limit of possible growth, being prevented from further extension by wave and ice action. In these places the forest is seen extending in its full development to a line where it ends abruptly, being separated from the water by a strip of nearly bare rock shore. At other points invasion is still actively in progress, and the transition from bare shore to mature forest is a gradual one. It is in such situations as these that the various stages in the succession are seen in their best development.

On all the types of rock shore, cliff and sloping, protected and exposed, of all kinds of rock, the successional stages and processes are in general essentially the same. There are, however, important modifications due to the differences in habitat just mentioned. Among them are telescoping, suppression, or elimination of certain stages, and variations in rapidity of invasion. In the following paragraphs the complete series of stages which constitute the rock shore succession will be first described, with the understanding that rarely will this series be found in absolute entirety. Afterward the modifications of the series associated with the different types of rock shores will be discussed.

a) The complete series

In tracing the early stages of the rock shore succession we find three separate lines of advance, which may conveniently be termed *subsuccessions*. They are the rock surface subsuccession, the crevice subsuccession, and the rock pool subsuccession. Later these unite, and the development proceeds thenceforth along a single line.

1. *The rock surface subsuccession.*—We have here mainly a study in the ecology of lichens, to which adequate treatment can be given only by a specialist in that group. The general sequence of stages has been frequently described in ecological papers, as by WHITFORD (**59**) for the southern shore of Lake Superior. Crustose lichens are the first plants to appear, and are accompanied by xero-

phytic mosses, principally *Grimmia ovata* Web. and Moore. A brilliant orange band of the lichen *Placodium* is a prominent feature of cliffs, its lower edge 2 m. above the water. This band is also distinguishable, though much less prominent, on the sloping shores. Next come foliose lichens, with the mosses *Hedwigia albicans* (Web.) Lindb. and *Orthotrichum anomalum* Hedw., and finally appear the fruticose forms, prominent among them the three large species of *Cladonia*, *C. rangiferina* (C.) Web., *C. sylvatica* (C.) Hoffm., and *C. alpestris* L.; also species of *Stereocaulon* (fig. 17).

FIG. 17.—Rock surface at Chippewa Harbor partially covered with a mat of cladonias; paucity of crevices resulting in very slow invasion; jack pines, pioneers of the xerophytic forest stage, in the background at the left.

The conditions on these bare surfaces are obviously severe, and without the aid of crevice plants vegetation advances very slowly upon them. Below they are frequently swept clean by the waves, and above, the wash of the rain keeps them clear of all débris except that of large size. Only in hollows can any gravel or humus accumulate, and only in such places does any moisture remain. As the lichen vegetation increases in bulk, soil and moisture are more and more conserved, and occasional herbs and low shrubs, and even trees, come in. Where there are few or no crevices, however, the process is so slow that such areas frequently become surrounded by mature forest, though the vegetation upon them may not have advanced as far as the heath-mat stage. Such "rock openings" are common in the forest upon the lower ridges. One of them, near Siskowit Lake (Sec. 32, T. 65 N., R. 35 W.), deserves description and illustration (fig. 18).

This opening was about 50 m. long by half as wide, and was surrounded by the climax forest, which ended rather abruptly at its edge. The surface of the rock was very smooth, little weathered, with very few crevices. A mat composed of mosses and cladonias covered it except for scattered irregular areas which bore only a few foliose and crustose lichens. The mat had started from numerous centers, forming at first more or less circular patches which later had partially coalesced. The thickest portions were composed principally of *Cladonia rangiferina*, *C. sylvatica*, and

FIG. 18.—Rock opening in the climax forest near Siskowit Lake: cladonias (lighter patches) are dominant; masses of the moss *Rhacomitrium* (darker areas) border the *Cladonia* patches; a few small areas of bare rock; *Cryptogramme acrostichoides* and other plants growing upon the mat.

C. alpestris, and around the edges of the patches and making up the thinner portions was a growth of the moss *Rhacomitrium canescens ericoides* (Web.) Schimp. Growing upon the thicker portions were scattered plants of *Cryptogramme acrostichoides*, *Diervilla*, *Arctostaphylos*, and a few others. The whole mat could be lifted from the rock, there being absolutely no connection except where the younger plants of the moss (*Rhacomitrium*) were feebly attached. This species was evidently the pioneer, and the cladonias later had become superimposed upon it. From this area we learn that a

luxuriant mat of vegetation may form upon a bare rock surface without the aid of crevice plants. The process, however, is exceedingly slow, and the mat thus formed is not so firmly attached and so surely permanent as that which is bound together by the trailing stems from the crevices.

2. *The crevice subsuccession.*—Crevices due to bedding planes, joints, and to differential weathering occur more or less commonly in all the rocks of Isle Royale. Where they are abundant the stages of the rock shore succession are passed through rapidly; where they are rare the process moves slowly. The soil which forms

FIG. 19.—*Potentilla tridentata* as a crevice plant; outer shore of Mott Island

in the crevices through disintegration of the rock, or is washed into them from the surrounding surfaces and the forest above, or is carried to them by the wind, is held within them, at least in part. Water flowing into or through the crevices also is retained. They form natural collecting places for seeds carried by wind, birds, and surface wash. Thus it is not surprising that nearly every crevice, large or small, is peopled by plants of many kinds. The number of species found growing as crevice plants is very great, and includes forms ordinarily occurring in diverse habitats. There are listed in my field notes 100 species, or one-fifth of the recorded flora of Isle Royale, as growing in crevices upon rock shores, and this list includes such forest plants as *Maianthemum canadense*,

Cornus canadensis, *Clintonia borealis*, *Mitella nuda;* and such bog forms as *Andromeda glaucophylla*, *Ledum groenlandicum*, *Aspidium Thelypteris*, and *Drosera rotundifolia*. Aside from these incidental occurrences, there is a group of species that inhabit crevices on the shores everywhere and which are rarely found in other habitats. By far the most important of the early arrivals on account of its abundance and densely tufted growth is *Potentilla tridentata* Ait. (three-toothed cinquefoil) (fig. 19). Other noteworthy pioneers are *Campanula rotundifolia* L. (bluebell), *Solidago hispida* Muhl. (goldenrod), *Achillea Millefolium* L. (yarrow), *Aster ptarmicoides* T. & G., *Saxifraga tricuspidata* Rottb. (three-toothed saxifrage), *Deschampsia caespitosa* (L.) Beauv. (hair grass), *Trisetum spicatum* (L.) Richter. Another group of plants deserves mention. These inhabit moist sheltered crevices and are also characteristic of the margins of rock pools. They are *Primula mistassinica* Michx., *Pinguicula vulgaris* L. (butterwort), *Selaginella selaginoides* (L.) Link, *Lycopodium Selago* L., *Polygonum viviparum* L. (alpine buckwheat), *Tofieldia palustris* Huds. (false asphodel), *T. glutinosa* (Michx.) Pers., *Parnassia palustris* L. (grass of Parnassus), *P. parviflora* DC, *Carex atrata* L. var. *ovata* (Rudge) Boott, *C. bicolor* All., *C. Halleri* Gunn., *C. paupercula* Michx. var. *pallens* Fernald, *Allium Schoenoprasum* L. var. *sibiricum* (L.) Hartm., *Empetrum nigrum* L. (crowberry), *Euphrasia arctica* Lange (eyebright), *Prenanthes racemosa* Michx. (rattlesnake root), *Calamagrostis hyperborea* Lange. Especially characteristic of moist cliffs are the mosses *Swartzia montana* (Lamk.) Lindb., *Tortula ruralis* (L.) Ehrh., *Encalypta procera* Bruch, *E. ciliata* (Hedw.) Hoffm. The result of occupation by these classes of plants is the accumulation of humus, with the accompanying decomposition of the adjacent rock.

With these plants, or usually somewhat later, come in certain low shrubs, among them two blueberries (*Vaccinium uliginosum* L. and *V. pennsylvanicum* Lam.). More important than these, in fact most important of all the crevice plants, are the trailing shrubs, the two junipers (*Juniperus horizontalis* Moench and *J. communis* L. var. *depressa* Pursh) and the bearberry (*Arctostaphylos Uva-ursi* (L.) Spreng.). With them should be included, although it

is ordinarily a tree, the arbor vitae (*Thuja occidentalis* L.), which frequently sprawls over the shore rocks after the manner of a prostrate vine.

Finally the trees also appear as crevice plants, and not always last in time, for young seedlings and even aged but stunted individuals are often found inhabiting the same crevice with the earliest herbaceous pioneers. Sometimes the largest cracks are lined with fair-sized trees while the rock surfaces between them are inhabited only by foliose lichens and cladonias. Any tree species may be a crevice pioneer, but *Betula alba* var. *papyrifera* occurs most frequently, with *Pyrus americana*, *Thuja occidentalis*, and *Abies balsamea* next in abundance. Growth in early years is sometimes of average rapidity, but the severe conditions soon make themselves felt, and those trees that survive increase in size very slowly. A white spruce 1 m. high and 8.75 cm. thick was found to be 87 years old, and a balsam of the same height but only 7.5 cm. thick showed an age of 123 years.

The preeminent importance of this subsuccession in the development of the forest should be emphasized. Through the soil and moisture-conserving capacity of the crevices and the resulting abundance and variety of their vegetation, and particularly because of the presence of creeping mat-forming shrubs, the establishment of the climax forest is very much hastened.

3. *The rock pool subsuccession.*—Much less important than the two preceding, but nevertheless contributing somewhat to the development of the forest by reason of the considerable amount of humus formed through its agency, is the rock pool subsuccession. Depressions of all shapes and sizes are common upon the rock shores (fig. 20). When they are of such a form as to contain standing water, the establishment of vegetation in them is quite different from that displayed in the crevices or upon the rock surfaces. Rain and waves furnish the water, which is frequently only temporarily present. The subsuccession is thus hydrarch in general but its development is subject to interruptions due to partial or entire desiccation. In the smaller depressions, which usually contain water only part of the time, vegetation when present is of the crevice type. In the larger basins which contain

pools that are nearly or quite permanent, the development is truly hydrarch; and zonation like that found in bogs, but of a simpler type, is usual. On account of the shallowness of the water the bog mat is seldom floating. By far the most important plant in the subsuccession is *Scirpus caespitosus* L., which starting its growth at the water's edge gradually fills the pools with its dense hard stools. Frequently by growing across the high water outlet it raises the level considerably. Other species are occasionally more important in filling the pools. For instance, one depression was found to be partially filled by a mat composed of *Polytrichum*

FIG. 20.—Rock pool upon one of the islands bounding Rock Harbor on the southeast: *Scirpus caespitosus* at the right; *Andromeda* and *Alnus crispa* at the left.

commune L. and *Aulacomnium palustre* (L.) Schwaegr., bound together by the roots and rhizomes of plants growing upon it, among them *Potentilla tridentata*, *Iris versicolor*, *Vaccinium pennsylvanicum*. Another pool was being invaded by a mass of *Climacium americanum* Brid. Upon the turf mat habitually lives the interesting group of plants which has already been listed as occurring in moist crevices. Bog plants are frequent, especially *Drosera rotundifolia* L. and *Polytrichum strictum* Banks; and numerous crevice plants occur. Following, usually, the building of the turf mat come certain shrubs, the most important being *Vaccinium*

uliginosum L. *Vaccinium pennsylvanicum*, *Andromeda glaucophylla*, and *Alnus crispa* also occur commonly. In some pools *Andromeda* is advancing directly into the water, the turf mat being absent. *Calamagrostis canadensis* (Michx.) Beauv. is usually a noteworthy companion to the shrubs.

4. *The heath mat.*—We have now traced the subsuccessions as far as they remain distinct. In the coalescence of the three the species of the crevice series are the active agents. Such plants as *Juniperus horizontalis*, *J. communis* var. *depressa*, *Arctostaphylos Uva-ursi*, and the *krummholz* form of *Thuja occidentalis* send out their trailing stems in all directions from the crevices in which they are anchored, winding through and among the cladonias of the rock surfaces and the various vegetation of the low places that were formerly pools. The continued growth of these three elements produces a firm compact mat, strongly attached in the crevices and depressions.

The history of an area may often be traced by an examination of the successive layers of the vegetation growing upon it. In one place four stages were discovered. Representing the first were scattered plants of *Potentilla tridentata* and *Deschampsia caespitosa* growing up through the mat and traceable to crevices in the rock beneath. Second in order was a thick layer of *Arctostaphylos* spreading over the rock in all directions but rooting in the crevices. The third stage was represented by *Juniperus horizontalis* growing over the *Arctostaphylos;* and the fourth by a few plants of the climax forest, among them *Aralia nudicaulis* and *Maianthemum canadense*. The order observed here is by no means universal; in fact, *Juniperus horizontalis* usually precedes *Arctostaphylos*.

The four important creeping shrubs differ greatly in their effectiveness in mat formation. In the case of *Thuja* the growth is too open and the branches reach too great an elevation above the surface to favor the accumulation of humus; and the same to a less degree is true of *Juniperus communis* var. *depressa*. *Juniperus horizontalis* by reason of its closely appressed habit is much superior. *Arctostaphylos* is probably the best of all, since its overlapping leaves almost entirely prevent the washing away of waste from beneath itself and other plants with which it grows. It is also

very effective as a conserver of moisture. When the soil elsewhere is absolutely dry, that beneath a layer of *Arctostaphylos* is often found still to contain a high percentage of water.

Vaccinium pennsylvanicum becomes of importance soon after the establishment of the mat, and frequently dominates large areas in which the junipers and *Arctostaphylos* appear as relicts only.

It must not be understood that there is a distinct belt of heath mat along the entire front of the forest, or even that it is commonly found continuously over very large spaces. It usually occurs in patches more or less united, separated by areas of bare or incompletely covered rock, and with scattered trees, invaders from the forest, growing upon it. Telescoping of stages is very pronounced in the rock shore succession, so that in a limited area we frequently find representatives of the earliest pioneers, the climax forest, and of all stages between.

5. *The jack pine-black spruce stage and the establishment of the climax forest.*—It seems clear that the climax forest often follows immediately after the establishment of the heath mat. It seems equally certain that in many places a relatively xerophytic forest stage intervenes, in which the species are *Pinus Banksiana* Lamb. (jack pine) and *Picea mariana* (Mill) BSP (black spruce). *Populus tremuloides* Michx. (aspen) is also sometimes present. The conditions which determine the presence or absence of this stage were not discovered. In either case the establishment of the forest consists simply in a gradual increase in the number of trees inhabiting the rocky shores, the early advance being principally along the crevices.

The jack pine-black spruce forest is at the present day rather limited in extent. It was observed in its best development along the southeast coast of the island from the region of Lake Whittlesey to Lea Cove, and along the northwest shore of Rock Harbor for several miles. In other localities transitional stages passing into the climax were seen. Where conditions are most xerophytic *Pinus Banksiana* is dominant. In such places the trees grow far apart and there is much bare rock visible between them. Cladonias are the characteristic ground cover, *C. rangiferina*, *C. sylvatica*, and

C. alpestris being about equally abundant. There is frequently considerable young growth of *Picea mariana* beneath the pines. The evidence derived from the examination of numerous localities indicates that such a type of forest will gradually become more mesophytic in character as the vegetation of the forest floor increases in amount and in water-holding capacity. Changes occur in the character as well as in the amount of the undergrowth. Mosses of the climax forest invade the areas dominated by the cladonias, growing around and over the masses of the lichens,

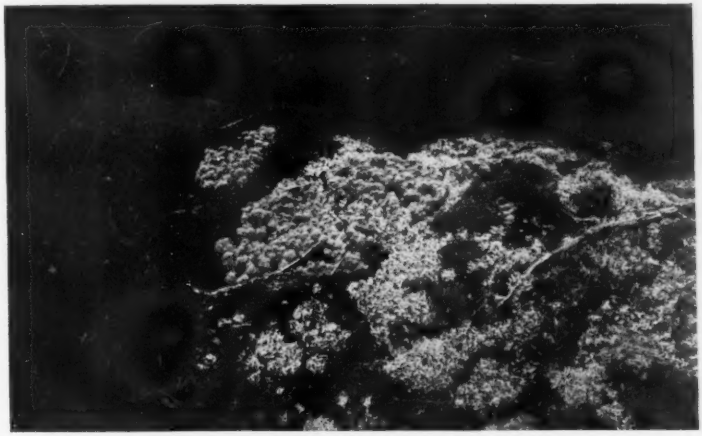


FIG. 21.—Ground cover in the jack pine-black spruce forest: the three cladonias of the heath mat (right), *C. rangiferina*, *C. sylvatica*, *C. alpestris*, invaded by the climax forest moss *Calliergon Schreberi* (left).

finally smothering them to death. *Calliergon Schreberi*, which among the forest mosses endures the driest conditions, is the most important of these (fig. 21). This species remains the most important element in the herbaceous vegetation throughout the intermediate forest stages, and frequently after the establishment of the climax type.

Picea mariana gradually increases, and at the same time the climax trees begin to be of importance. Here too the phenomenon of telescoping is to be seen, for we seldom find an area of jack

pine-black spruce forest that is pure; that is, where there is not present a more or less important element representing the climax stage.

The penultimate stage in the succession is quite frequently seen. The jack pine has disappeared and the black spruces are present mainly as relicts. *Calliergon Schreberi* has come to share its position of dominance with the more mesophytic mosses *Hypnum cristacastrensis* and *Hylocomium proliferum;* and the climax trees have assumed their characteristic relations.

b) Effect of special conditions upon the rock shore succession

The shore vegetation as we see it today has not everywhere the same aspect, and the differences that appear are explained by the operation of the two following laws.

1. *The lower limit of possible forest extension is determined approximately by the upper limit of effective wave and ice work, the lake level remaining constant.*—The limit varies from the water level along the sheltered coves and harbors to a height of several meters upon the shores that face the lake. It is here far above the reach of the highest waves of the growing season, since the most severe storms take place during late fall and early winter (see ADAMS **4**, p. 46). While depending in the main upon the size of the waves that break upon it, the position of the limit of forest extension is modified by the character of the shore. If it be rough or broken by ledges, neither waves nor ice will be projected so far as if the slope were smooth and unbroken, and the forest in the former case may thus establish itself lower. The effects of such differences may be seen by comparing figs. 15 and 27. If by reason of a gentle submarine slope or a submerged reef the waves break far from shore, the limit of forest extension may be greatly lowered.

2. *The extent to which the forestable territory has been occupied at the present day depends upon the rapidity of invasion, which is governed by the character of the rock, the angle of slope, and the degree of exposure to winds.*—Abundance of irregularities and crevices in the rock surface and the presence of large quantities of the products of disintegration tend to facilitate invasion, while smoothness of surface, paucity of crevices, and freedom from disintegration prod-

ucts retard it. On a steep slope soil materials and seeds as well are washed away to a greater extent than on a gentle one. The effect of wind in opposing invasion consists in the drying out and blowing away of the small but valuable deposits of humus which accumulate upon the rocks, in the uprooting of scattered trees feebly anchored in the shallow soil, in the breaking off of those more firmly established, and in the increase of the evaporation rate.

The effects of these factors are seldom or never strictly separable, but in various combinations they result in the production of three

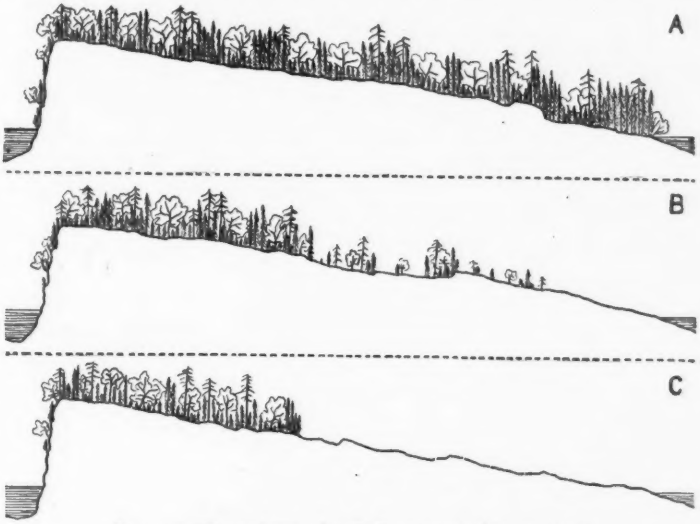


FIG. 22.—Three phases of rock shore vegetation; see text

phases of rock shore vegetation, differing from each other in respect to the position of the limit of forest extension and in the extent to which the forestable territory has been occupied. These are illustrated in the diagram (fig. 22). Both sides of the island represented are assumed to be equally exposed to wind and waves.

A represents an island which is effectually sheltered from the lake storms. Shores such as these are characteristic of the inner coves and harbors of Isle Royale. Upon the gentle slope at the right the climax forest in full development has reached the water's

edge, and a fringe of *Alnus crispa* overhangs the bank (fig. 23). Upon the cliff at the left (fig. 22) the forest has also reached the lake level, but the trees are necessarily far apart, growing only where ledges or large crevices give them foothold. Wave action being at a minimum, the limit of possible forest extension is at the water's edge, and the conditions of surface, slope, and exposure to wind being favorable, all of the forestable territory has been occupied.

B represents the phase which is perhaps the commonest upon Isle Royale, and which shows to best advantage the various stages

FIG. 23.—Thoroughly sheltered shore of type *A:* forest to the water's edge; southeast side of Blake Point peninsula.

that make the complete rock shore succession. The limit of possible forest extension may be at the water's edge or at any line above it, according to the degree of exposure. Back of this limit there is a zone where occupation has been more or less incomplete, because of one or more of the retarding influences, unfavorable character of the rock, steep slope, and exposure to winds. The manner of invasion is plainly seen upon such shores. As we pass downward from the climax forest the trees become continually sparser and smaller, and the undergrowth more xerophytic. As we go farther only scattered trees are seen, closely confined to the crevices, and

the intervening spaces are covered with heath mat or are partially bare. The outermost pioneers of the forest may or may not have reached the limit of its possible extension. Such a shore is illustrated in fig. 24.

Although as we pass outward the trees become less frequent and smaller, there is no corresponding decrease in age. The outermost individuals are often as old as any in the fully developed forest. The process of invasion in a given spot is a matter of much longer duration than a generation or two. Tree after tree lives its life in the same crevice and finally succumbs to the severity of the

FIG. 24.—Shore of type *B:* gradual invasion; island near Blake Point

conditions, each contributing toward the development of the future forest only the small remnant of humus resulting from its decay that is not blown or washed away. Through successive generations the number of individuals living at the same time slowly increases, until the assemblage of trees attains the character of true forest.

Certain of the larger rock openings upon the forested ridges, now 20 m. or more above the water, have not yet lost their resemblance to the shores, in spite of the dozens of centuries that have passed since the lake stood at their level. Such an opening (Sec.

33, T. 67 N., R. 33 W.) is shown in fig. 25, and the extraordinary likeness to the shore illustrated in fig. 24 will at once be evident.

An especially interesting feature of this locality is the fact that just below the opening and extending to the water's edge of Tobin's Harbor is an area of climax forest of unusual beauty. The explanation of this is found in the physiographic history of the island. When the area of the present rock opening was actual shore the waves of the open lake broke upon it. As the water level subsided the ridge of Scovill Point appeared, affording full protection to the

FIG. 25.—Rock opening on the southeast slope of the Greenstone Range near Tobin's Harbor: when Scovill Point (right, in the distance) was submerged, this was a shore area exposed to the open lake; note likeness to fig. 24.

new shore area along the northwest side of Tobin's Harbor. Upon this latter, protected from both waves and wind, and receiving all the soil materials washed down from the slope above, invasion went on rapidly, resulting in the speedy establishment of the climax forest. The area higher up, exposed to the full force of the winds sweeping in from the lake across Scovill Point, still lingered in the early stages of the succession.

QUADRAT 7 (fig. 26) was located in the large rock opening described above. The likeness is so great that it may be taken also as representing shore conditions of type *B*. The surface of the

rock was considerably disintegrated, and on areas not covered by the heath mat bore a rich lichen vegetation, the most important species, as usual in the late lichen stages, being the large cladonias. In the heath mat *Juniperus communis* var. *depressa* was dominant,

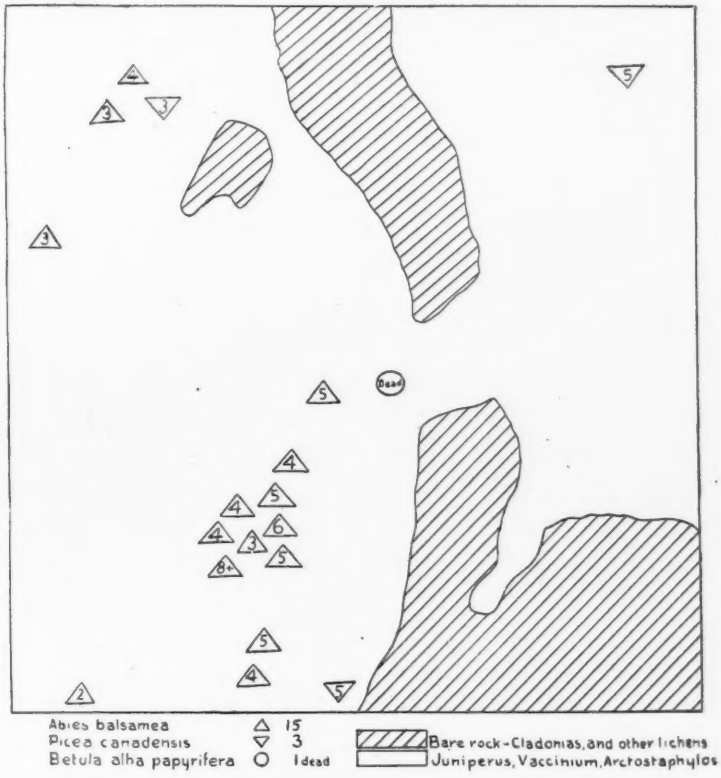


FIG. 26.—Quadrat 7: in same rock opening as fig. 25; also illustrates shore conditions of type *B;* for explanation of symbols see fig. 6.

and *Juniperus horizontalis*, *Vaccinium pennsylvanicum*, *Arctostaphylos Uva-ursi*, and *Calliergon Schreberi* shared in its composition. Crevice plants were frequent and forest herbs occurred sparingly. Undrained depressions were filled with *Aulacomnium palustre* (L.) Schwaegr. and *Scirpus atrocinctus* Fernald. These

in earlier times may have been rock pools. Turning to the trees, we find representatives of the three climax species and no others in this particular spot. There is thus no xerophytic forest stage here, although near by scattered individuals of *Pinus Banksiana*, *Picea mariana*, *Populus tremuloides*, and *Thuja occidentalis* were noted. Balsam, the most abundant tree of the climax forest, is even here the dominant species, and this is true of the rock shores in general. None of the trees have attained great age, 50 years being the average. The rate of growth was found to vary greatly,

FIG. 27.—Shore of type *C*: limit of forest extension very high, due to exposure and smoothness of slope; note abrupt transition from bare shore to forest; one of the islands bounding Rock Harbor on the southeast.

those happily situated in regard to soil, moisture, and competition having wider rings than the less favored ones. In the rather close group below the center of the quadrat, due to a crevice, suppression was already evident, a few individuals, most of them slightly older than the others, being large and well formed, while the rest were small and stunted. Occasional standing dead trunks and frequent decayed logs remained as evidence of former generations.

C (fig. 22) represents the third type of shore, which is common along the most exposed portions of the southeast coast (fig. 27). The distinctive feature is the abruptness of the transition from

the nearly bare rock surfaces on which the early lichens and crevice plants are almost the only vegetation, to the climax forest in its full development. Intermediate stages are often entirely lacking. The causes that bring about this abrupt transition are as follows. On account of the immediate proximity of the open lake the limit

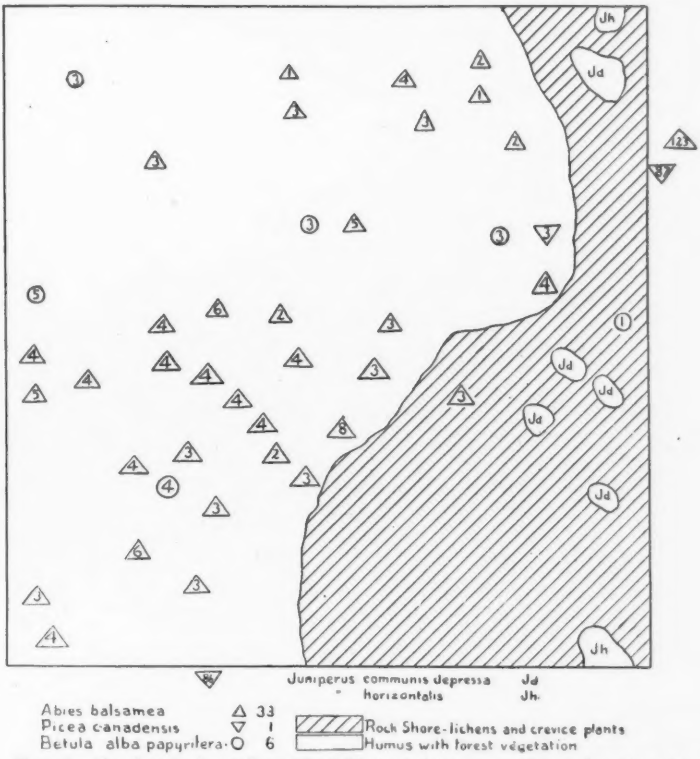


FIG. 28.—Quadrat 8: located on island illustrated in fig. 27; for explanation of symbols see fig. 6.

of possible forest extension is very high. Above this line invasion has been sufficiently rapid to bring about the development of the climax forest upon the whole of the forestable territory. The intermediate stages have been "pinched out," as it were, by the advance of the climax forest against the impregnable barrier of the waves and ice.

A small portion of such a shore is shown in quadrat 8 (fig. 28). It was located on a small island of the outer row (Sec. 35, T. 67 N., R. 33 W.), the same that is shown in fig. 27. The line of demarcation between forest and shore is here more definite than usual, being emphasized by the presence of a slight inward-facing cliff which affords some degree of protection to the area behind it. The shore portion of the quadrat is in a rather early stage of development, the only indication of future mat formation being the patches of the two junipers shown upon the diagram, and a few scattered plants of *Arctostaphylos* and *Vaccinium pennsylvanicum* in the crevices. The forested portion might have been taken as an excellent example of the climax type. A striking feature is the zone bordering the shore area thickly peopled with young trees, mostly balsams. This is a consequence of many windfalls, resulting from excessive exposure. The spruce and balsam just outside the quadrat on the lakeward (right) side show the tenacity with which trees occasionally persist under the severest conditions, if deeply and firmly anchored in crevices. These were low scraggy individuals, very small in diameter considering their age, being respectively 8.75 and 7.5 cm. thick, and 87 and 123 years old.

c) Possible differences in the rock shore succession during the early history of Isle Royale

It must not be understood that the processes which are going on now are necessarily exactly like those that have been in operation during previous periods of the island's history. Many species, now of considerable importance, doubtless arrived upon the island long after its first emergence, and without these the balance of power may have been very different. There is no reason, however, for supposing that in their essential features the successions of the past have differed greatly from those of the present. A suggestion of what the earliest vegetation may have been, at the time when Isle Royale was merely a line of reefs barely above the surface of Lake Duluth, was obtained from a study of Gull Islands, 13 km. northeast of Blake Point. There appeared some surprising differences from the normal rock shore succession as seen upon Isle Royale itself, and the effect of the animal life upon the flora was noteworthy.

Gull Islands.—These are a line of rocky knobs rising 1.5–12 m. above the surface of the water. They are projecting points of the Greenstone Ridge which disappears under the water at the northeast end of Isle Royale, reappears in Passage Island, and again here.

They are steep-sided in the main, and at one point on the northwest side of the largest islet there is a small shingle beach. As the name indicates, the islands are favorite haunts of the herring gulls, which congregate and breed here in enormous numbers. They are accompanied by many smaller birds and by untold millions of flies and gnats, evidently living upon the decaying animal matter, which is abundant and offensive.

The vegetation was found to be a strange mixture of shore and forest plants, the latter in spite of the bareness of the islands including some that habitually grow in deep shade. There were also other species which belonged to neither category. Wherever conditions favored accumulation, humus was deep and seemed to be composed largely of the remains of *Calamagrostis canadensis*, the most abundant species upon the islands. In some places this grass formed a thick rank growth, flowering abundantly. Over large areas there was merely a short turf, and in many places the humus was entirely bare, doubtless kept so by the gulls in their domestic operations. With *Calamagrostis* and forming a thicket-like growth was found *Pyrus americana*, and this was the only tree upon the islands. It was most abundant upon the upper part of the beach mentioned above, where a few specimens were noted that were 4 m. high and 1.5 dm. in diameter (fig. 29). There were more dead specimens than live ones, and the living showed the effects of the hard conditions in yellow and curled foliage and dead branches. Fruit was borne abundantly. Other shrubs that formed a part of the thicket were *Salix phylicifolia* L.; *Cornus stolonifera* Michx. (red osier dogwood); *Ribes prostratum* L'Her (fetid currant), fruiting in wonderful abundance; *R. oxyacanthoides* L. (prickly gooseberry); *Rosa acicularis* Lindl. var. *Bourgeauiana* Crépin; *Rubus idaeus* L. var. *aculeatissimus* (C. A. Mey.) Regel & Tiling (red raspberry), abundant; *Sambucus racemosa* L. (red-berried elder); *Taxus canadensis* Marsh (ground hemlock), frequent, forming a low matted yellowish growth partially protected

by other shrubs; most surprising of all, *Fatsia horrida* (Sm.) B. & H. (devil's club), about six specimens with curled and yellow leaves, but all flowering.

In all, 26 species were listed, and of these only 5 are characteristic shore plants; 10 were species found ordinarily in the climax forest, but growing here with more or less success in spite of the severe conditions. The way in which many of the plants reached the island is suggested by the fact that 10 out of the 26 bear more or less edible berries. Birds have evidently been important agents in determining the composition of the flora of Gull Islands.

FIG. 29.—One of the Gull Islands: a small shingle beach with stunted mountain ash; with this grew a few plants of devil's club (*Fatsia*).

Such a type of vegetation as exists today upon these rocks may well have been the first to occupy the summits of the Isle Royale ridges when they first emerged from Lake Duluth. As the area of the island increased, and more and more species became established upon it by various means, the vegetation of the shores and the successional processes concerned therein became gradually like those of today.

III. The beach succession

a) Extent, situations, and materials of the beaches.—Beaches are numerous but not extensive upon Isle Royale. There are many

miles of rocky coast absolutely unbroken by beaches of any kind. Wave erosion at the present lake level has not yet produced an irregular coast line, in the reentrants of which they might develop, nor has it furnished abundance of sand, gravel, and shingle for their building. The general steepness of the shores is another unfavorable feature. Such as are present occur in the bays and coves, most of which are due not to wave erosion but to the original configuration of the rocks. The fragments eroded from the bold cliffs and headlands near by are swept into these reentrants and come to rest there in the comparatively quiet water. Most of the beaches are of limited extent, but at the head of Siskowit Bay there are two magnificent stretches, separated by Senter Point, which have a total length of 2 km. The materials range from fine sand to coarse shingle, the larger sizes being by far the commoner. Back from many of the present beaches extend similar accumulations which were made when the water level stood higher than now, and formations identical in character occur at various levels upon the ridges.

b) *Vegetation.*—From their nature, beaches occupy situations that are more or less protected from the full force of waves and ice, and usually from wind also by reason of neighboring headlands. As compared with the rock shores they thus provide favorable opportunity for invasion by plants. The limit of possible forest extension, as in the case of the rock shores, varies with the effective reach of waves and ice, but is never high. Below this limit the materials are frequently moved about by the waves, and all vegetation except annuals is manifestly impossible. Even lichens must be destroyed by the movement and friction. Above the limit of the waves, where the fragments are not disturbed, conditions are particularly favorable for invasion. If the material is fine a soil is already present, if coarse there is opportunity for the accumulation of soil in the interstices of the shingle. In the latter case water drains off too rapidly, but as the openings become filled, this fault is gradually corrected.

Because of the favorable conditions enumerated above, the climax forest in most cases has already advanced to its limit of possible extension. Very often a bank of solid humus, formed

during long ages of forest growth, marks the upper boundary of the beach. The transitional stages have thus been pinched out, and opportunities for their investigation are therefore scanty.

Where the forest ends most abruptly a line of *Alnus crispa* commonly fringes it (fig. 30). Where the transition is slightly more gradual there are suggestions of intermediate stages. Out among the shingle are found scattered herbs: *Equisetum arvense* L. (horsetail), *Epilobium angustifolium* L. (fireweed), *Deschampsia caespitosa* (L.) Beauv. (hair grass). *Rubus triflorus* Richards (dwarf raspberry) often trails over the stones for many decimeters. A more important group is made up of low shrubs, among which *Rubus idaeus* var. *aculeatissimus* (red raspberry), *Diervilla Lonicera* Mill (bush honeysuckle), *Rosa acicularis* Lindl., *Physocarpus opulifolius* (L.) Maxim. (ninebark), and *Rubus parviflorus* Nutt. (white-flowered raspberry) are most prominent. Behind these come the tall shrubs, *Alnus crispa* most important, and also *Cornus stolonifera* and several species of *Salix*. No instance of actual transition into the climax forest was observed, but it probably follows immediately after the tall shrubs.

FIG. 30.—Upper limit of shingle beach on the northwest side of the Blake Point peninsula: note large size of material; *Alnus crispa* fringing the forest.

PALO ALTO, CALIFORNIA

MACROZAMIA MOOREI, A CONNECTING LINK BETWEEN LIVING AND FOSSIL CYCADS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 168

CHARLES J. CHAMBERLAIN

(WITH TWELVE FIGURES)

The greatest cycad centers of the world are the states of Vera Cruz and Oaxaca in Mexico and Queensland in Australia, Queensland having three genera, *Cycas*, *Macrozamia*, and *Bowenia*, and the Mexican region three genera, *Dioon*, *Ceratozamia*, and *Zamia*. As yet no other region has claimed more than two genera. In the cycad region of Australia *Macrozamia* is the dominant genus, and its various species range from the northern part of Queensland to the southern limit of cycads in New South Wales. In a more extended publication the genus and the interrelationship of its species will be discussed, but at present we shall consider only a single species, *Macrozamia Moorei*, which presents features of unusual interest. The field study was made at Springsure, about 200 miles west of Rockhampton and almost on the Tropic of Capricorn.

Macrozamia Moorei has a massive cylindrical trunk with a splendid crown of leaves (fig. 1). Most of the plants grow in the blazing sun, but some are found in the scanty shade of small *Eucalyptus* and other trees. The altitude of Springsure is about 325 m., but some plants were noticed a few miles east of Springsure, perhaps 30 m. lower, and specimens could be seen on the tops of the neighboring mountains, perhaps 300 m. higher.

The trunk is 2–3 m. high in most of the large plants; a few reached 5 m. in height, and one specimen, growing in the shade, measured 7 m. from the ground to the bud. The diameter of the trunk of this specimen was 66 cm., but there is little increase in diameter after a plant reaches a meter in height, for such plants may be 0.5 m. in diameter, and some plants 3 m. in height, and growing in the sun, measured 71 cm. in diameter.

The foliage display is not surpassed by any cycad. The leaves are 2–3 m. in length and may number more than 100 in a single crown. With so many large leaves in a crown, and, in all probability, a new crown nearly every year, the trunk grows rapidly. Mr. J. W. KEIT, of Durban, South Africa, showed me an ovulate plant raised from a seed planted 30 years before, which had a stem reaching 25 cm. above the surface and bearing a fine crown of leaves and two large cones. Another plant, also raised from a seed

FIG. 1.—*M. Moorei* at Springsure: ovulate plant in foreground has trunk about 3.5 m. in height.

planted a few years before the one just mentioned, had a stem 40 cm. in height and had borne ovulate cones for several years. This shows that the plant grows very rapidly and produces cones at an early age. Although it is very probable that small cycads, like *Zamia*, produce cones at a still earlier age, this is the first instance, so far as I know, in which the period between the planting of the seed and the production of cones is known, even approximately.

The armor of leaf bases persists even at the base of the stem, so that the age of a plant could be estimated quite easily, if it were

known how often new crowns are produced. If crowns are produced every year, a plant a meter in height might be considerably less than 100 years old.

Although the trunk is so massive, a transverse section shows the large pith, scanty wood, and large cortex, so characteristic of cycad stems, there being no extensive development of wood like that found in large stems of *Dioon spinulosum*. A plant about 3 m.

FIG. 2.—*M. Moorei:* transverse section of stem 45 cm. in diameter

in height, with a stem 45 cm. in diameter, had a zone of xylem and phloem only 5 cm. in width (fig. 2). In the photograph three distinct regions are shown; the innermost is the xylem, the middle one its accompanying phloem, and the outermost a second cylinder with its xylem and phloem which show clearly in the material but which are not differentiated in the photograph. The trunk, therefore, is polyxylic. The outer cylinder evidently originates in the cortex, as in *Cycas*, but is separated from the primary cylinder by only a scanty amount of parenchyma. There are

scattered bundles in the pith, but there are no cone domes, and the scattered bundles seem to have no connection with cones. In regard to the bundles in the pith, this stem is somewhat like that of *Macrozamia Fraseri*, as described by WORSDELL.[1]

The tracheids of the xylem show two, three, or four rows of crowded bordered pits. There are uniseriate rays, similar rays two or three cells wide, and large rays containing vascular strands,

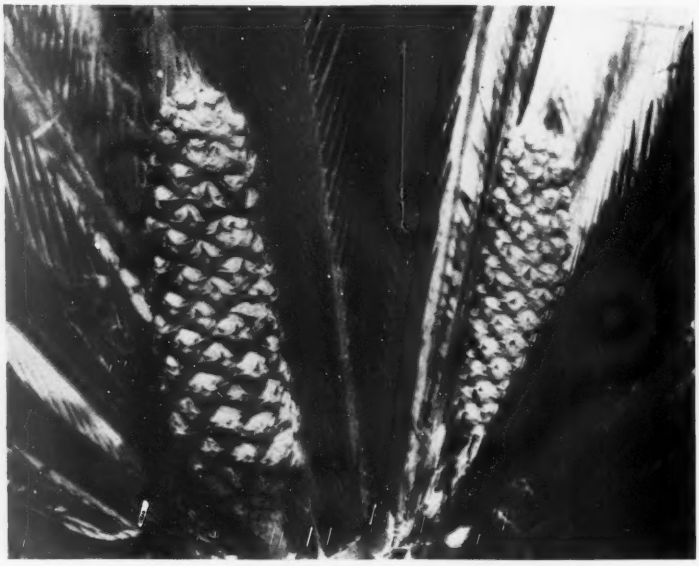


FIG. 3.—*M. Moorei:* ovulate cones about 76 cm. in length

as in *Dioon*. There is no more difference between the general and histological structure of the stems of *Macrozamia* and *Cycadeoidea* than may be found between different genera of Cycadales. Bennettitales and Cycadales could hardly be separated on the basis of stem structure.

The ovulate cones are large and are seldom borne singly, two, three, or four being more common than a single cone, and in one case

[1] WORSDELL, W. C., Anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. Ann. Botany **10**: 601–620. *pls. 27–28.* 1896.

I saw eight large cones on a single plant (fig. 3). When I visited Springsure, late in November, the cones were not mature, but some of them were already 80 cm. in length and weighed 15 kilos. Dr. F. M. BAILEY, in his *Flora of Queensland*, reports cones 90 cm. in length. Scarcely any of the cones were vertical, nearly all leaning and some of them almost horizontal (fig. 1). The numerous strong leaves prevent the cone from hanging down, as it does in *Dioon spinulosum*.

FIG. 4.—*M. Moorei* with more than 50 staminate cones

By far the most striking feature of *Macrozamia Moorei* is its staminate cones and associated structures (fig. 4). Plants with 20–40 staminate cones were not at all rare, and in one case I counted 103 cones on a single unbranched plant. Not only is the number larger than has ever been reported for any cycad, but the cones are obviously lateral, as may be seen by a glance at the figure, which shows a girdle of cones outside the new crown and scattered among the leaves of the previous crown. Young cones of the next season are found among the bases of the leaves of the new crown, but there are no cones in the center of the crown.

A tangential section through the armor at the top of the stem (fig. 5) shows a condition exactly like that seen in WIELAND'S figures of *Cycadeoidea*. The peduncles of the cones, with their accompanying scale leaves, are wedged in among the leaf bases, and sections show that the cones arise in the axils of the leaves. Of course, the terminal peduncles of *Dioon* and similar forms finally become wedged in among the leaf bases, but the condition is secondary and is due to the sympodial nature of the stem; in

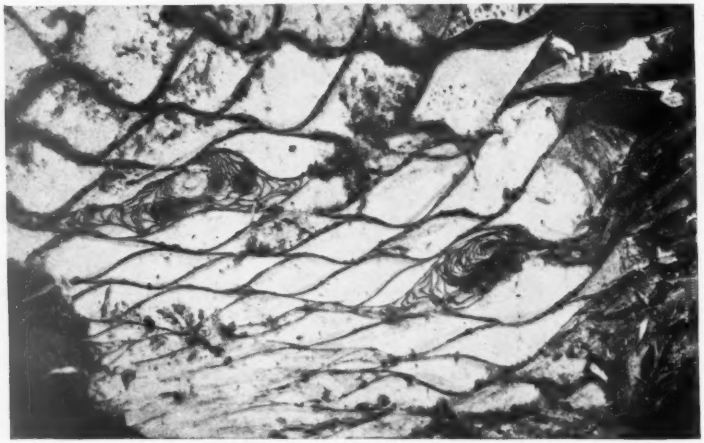


FIG. 5.—*M. Moorei:* tangential section (cut with an ax) through the armor of leaf bases, showing the peduncles of cones surrounded by scale leaves.

Macrozamia Moorei the condition is primary, the stem being monopodial, with all its cones lateral.

In all the occidental cycads, *Dioon*, *Ceratozamia*, *Microcycas*, and *Zamia*, a single ovulate cone is a rule to which there are scarcely ever any exceptions, except in *Zamia;* in staminate plants exceptions are almost as rare, except in *Zamia*, which very frequently has more than one cone, and sometimes as many as six or seven. In *Dioon*, *Ceratozamia*, and *Zamia*, in both ovulate and staminate plants, the cone domes in the pith indicate the sympodial nature of the stem. *Microcycas* has not been examined, but will doubtless show cone domes.

Among the oriental cycads (*Cycas*, *Macrozamia*, *Bowenia*, *Encephalartos*, and *Stangeria*) the situation is not so uniform. In *Cycas* the ovulate plant does not bear a compact cone, the sporophylls having the position of a crown of vegetative leaves with the growing point at the center, the growing point persisting from the seedling throughout the life of the plant. In the staminate plant there is hardly ever more than one cone, and this is terminal. There are cone domes in the pith.

In *Bowenia*, both ovulate and staminate cones are borne singly on slender branches of the main stem.

In *Stangeria*, both ovulate and staminate cones are terminal and are usually borne singly, although occasionally there may be two or three, especially in case of staminate plants. There are well marked cone domes in the pith.

In *Encephalartos*, both male and female plants often bear more than one cone, and in some species a single cone is the exception, while three, four, and five are common. PEARSON noted that in *Encephalartos Frederici Gulielmi* the cones are arranged in a circle about the bud. In this species, at Queenstown, South Africa, where PEARSON made his observation, I saw seven ovulate cones in a circle about a well developed bud. In *E. caffer*, *E. Altensteinii*, *E. horridus*, and *E. villosus* I found three to five cones in a circle about a well developed bud. Such cones are lateral with respect to the growing point, which does not become transformed into a cone, but continues the growth of the plant. A dissection of adult specimens of *E. Altensteinii* and *E. villosus* showed no cone domes in the pith, and cone domes are necessarily present when cones are terminal. It may be doubtful whether cones are terminal in *Encephalartos*, even when produced singly.

In various species of *Macrozamia* ovulate plants frequently bear more than one cone, and in staminate plants more than one cone is the rule. Both ovulate and staminate cones are obviously lateral, even when borne singly. There are no cone domes in the pith.

Of course, in all the genera, when there is branching in the popular sense of the term, each branch may bear a cone.

Since *Macrozamia Moorei* approaches so closely to the Ben-

nettitales, it is worth while to consider how a compact cone has probably been derived from a loose crown of sporophylls, and how the terminal position of cones may have succeeded the lateral. The compact cone, found everywhere in living cycads, except in the ovulate plant of *Cycas*, has in all probability been derived from a loose crown of sporophylls like those of the Cycadofilicales and the staminate sporophylls of Bennettitales, and like the ovulate sporophylls of *Cycas*. Various species of *Cycas* show stages in the advance from this loose crown of leaflike sporophylls toward the compact cone composed of sporophylls so highly modified that their leafy nature is very much obscured. In *Cycas revoluta* the sporophylls are quite leaflike and bear five or more ovules; in *C. circinalis* the pinnae are much more reduced, appearing only as serrations on the edge of the much reduced blade; in *C. media* the sporophyll is equally reduced and frequently bears only two ovules; in *C. Normanbyana* the sporophyll is about as in *C. media*, but there are regularly only two ovules. From the sporophyll of *C. Normanbyana* to that of *Dioon edule* the transition is easy, and the loose cone of *D. edule* does not differ much in appearance from early stages in the development of the ovulate structures of *Cycas*. The distinguishing feature is that in the ovulate plant of *Cycas* the meristem never becomes converted into sporophylls, but continues the growth of the axis. From the condition in *Dioon* to the more compact cones of the remaining genera, the transition is easier still, and consists principally in shortening the blade of the leaf until it finally reaches the almost peltate sporophyll of *Microcycas* and *Zamia*. Occasionally a proliferating cone reminds one of the *Cycas* condition.

In the reduction of the number of cones, and in the evolution of the compact cone from a loose crown of sporophylls, we have two independent series of changes, which may or may not have progressed with equal rapidity. Loose staminate sporophylls and numerous lateral cones are characteristic of the Bennettitales. The combination of loose sporophylls and numerous lateral cones is not found in any living cycad, but loose sporophylls are found in the ovulate plant of *Cycas*, and numerous lateral cones are found in *Macrozamia Moorei*, the staminate cones being almost as numerous

as in Bennettitales; while in other species of *Macrozamia* and in *Encephalartos* the lateral cones are present but not so numerous. In a reduction from numerous lateral cones to a single cone, the natural limit would be the single terminal cone developed from the apical meristem, and with the transformation of the apical meristem into a cone, the formation of a cone dome in the pith would be a necessary consequence. Accordingly, the absence of cone domes from *Macrozamia* and *Encephalartos* is easily understood.

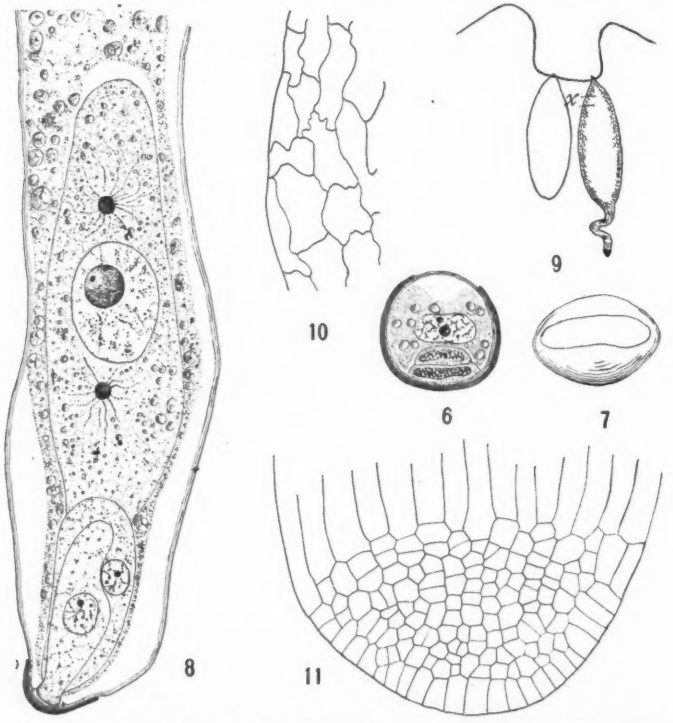
Macrozamia Moorei, in its numerous lateral cones and in their mode of occurrence, presents a condition identical with that found in *Cycadeoidea* among the Bennettitales. As far as the mode of bearing cones is concerned, *Macrozamia Moorei* makes the transition from Bennettitales, like *Cycadeoidea*, to the modern cycads an easy one. In the structure of the individual cone, the transition is not so easy, but may become less difficult when more is known about the cones of the Bennettitales, especially the lower Bennettitales. The connection between the higher Bennettitales and the Cycadales, already a close one, is made still closer by *M. Moorei*, so that it might be doubted whether the differences are great enough to distinguish orders.

The male gametophyte

The pollen grain at the time of shedding contains three cells, a persistent prothallial cell, a generative cell, and a tube cell (fig. 6). As pollen shaken out from the cone loses a little moisture, it begins to collapse so that in a vertical view the grains appear elliptical, with a long narrow area at the top which does not stain when safranin is added (fig. 7). This elongated area becomes narrower as the grain dries and finally the sides come into contact. A study of sections shows that this elongated area at the top of the grain is not covered by the exine, but only by the intine, a situation which is constant in *Ginkgo*, but which has not been noted in cycads. Just beneath the portion not covered by exine there is usually a funnel-shaped depression. The cytoplasm of the pollen grain is quite dense and contains starch.

The pollen from which figs. 6 and 7 were drawn was shaken from a cone in the Botanic Gardens at Sydney on November 3, 1911,

and the condition of the staminate cones in the field at Springsure, about 1100 miles farther north, on December 1 would indicate that in the field the pollen had been shed at about the same time, or perhaps a little earlier. On December 1 the generative cell has



FIGS. 6–11.—*M. Moorei:* fig. 6, pollen grain at the shedding stage, November 3, 1911, showing prothallial cell, generative cell, tube cell, and starch grains; ×800; fig. 7, pollen grain; the elongated area is not covered by exine; ×800; fig. 8, pollen tube, December 1, 1911; ×480; fig. 9, upper part of female gametophyte, February 1912, showing deep archegonial chamber and young embryo; ×6; fig. 10, portion of parietal tissue of proembryo at *x* of fig. 9; ×130; fig. 11, tip of embryo shown in fig. 9; ×58.

already divided, forming the stalk and body cells, and the blepharoplasts have appeared (fig. 8). The pollen tube structures at this stage are about as in *Dioon*, there being scarcely any branching of

the tube and none of the peculiar basal haustoria which characterize the pollen tubes of *Ceratozamia*.

The condition of the male gametophyte when the pollen is shed is remarkably uniform in the family, no exception to the three-celled stage having as yet been demonstrated. IKENO found this condition in *Cycas revoluta*, and Miss FRANCES G. SMITH found it in *Encephalartos villosus*. I have observed it in *Dioon edule*, *Ceratozamia mexicana*, *Microcycas calocoma*, *Zamia floridana*, *Bowenia spectabilis*, *Macrozamia Miquelii*, *M. spiralis*, and *Stangeria paradoxa;* so that it occurs in all the genera. The behavior of the three cells is also similar, the prothallial cell pushing up into the stalk cell in all the genera, with the possible exception of *Cycas*.

Since the structure of the pollen grain is so uniform in the cycads, it would be interesting to know just what the structure is in fossil Cycadales and Bennettitales. A more extensive development of prothallial tissue and a comparatively slight development of the pollen tube or haustoria might be anticipated.

The female gametophyte

Early in November, when the ovulate cones have attained a length of 78 cm., the female gametophyte has reached its full size, but by no means its full density. The archegonia, generally 4–6 in number, are a little more than 3 mm. in length and are becoming filled with protoplasm and foodstuffs. The ventral canal nucleus has not yet been cut off and the archegonial chamber has just begun to develop. At the fertilization stage, most of the cells of the female gametophyte contain large starch grains; the rest contain tannin. The archegonial chamber is the deepest ever noted in a cycad, the average depth being about 1.8 mm., so that the depth is nearly two-thirds as great as the length of the archegonium (fig. 9).

The embryo

The earlier stages in the development of the embryo are not available, but arrangements have been made to secure them. The earliest stage in our material is shown in fig. 9. At this stage *Macrozamia Moorei* differs from *Dioon edule*, *Ceratozamia mexicana*, and *Zamia floridana*, but agrees with *Cycas revoluta* and perhaps

with *C. circinalis*. In *Zamia* and *Ceratozamia* fertilization is followed by a series of free nuclear divisions and finally cell formation takes place only at the bottom of the egg, less than one-fifth of the egg becoming segmented, while the rest remains in the free nuclear condition. In *Dioon edule* the free nuclear stage is followed by an evanescent segmentation of the entire egg, but later

FIG. 12.—*M. Moorei:* a poisoned plant

stages show segmentation only at the bottom of the egg, with free nuclei above. *Macrozamia Moorei*, in the only stages available, shows complete segmentation, but a large vacuole has already developed, and within the limits of the egg there remains only a cellular layer two or three cells in thickness (fig. 10). Material of *Cycas revoluta* in this stage, furnished me by IKENO several years ago, shows exactly this condition. Whether both have passed through a stage of complete segmentation, as in *Ginkgo*, or segmentation

has occurred only at the periphery, the vacuole having been formed by the breaking down of free nuclear material, are questions which could be answered by a glance at material in the desired stages. The extensively segmented proembryos of *Macrozamia* and *Cycas*, and even the temporarily segmented proembryo of *Dioon*, are, in our opinion, more primitive than the proembryos of *Zamia* and *Ceratozamia*, which are segmented only at the base.

At the stage shown diagrammatically in fig. 9 and quite accurately in fig. 11, the differentiation into suspensor and embryo proper is quite distinct, but there is not yet any differentiation of plerome and periblem or even dermatogen; the outer layer of large absorbing cells still showing numerous periclinal divisions.

Unfortunately, the young leaves of *Macrozamia* contain a poison which causes a kind of paralysis in cattle, and consequently the plant is in bad repute among cattlemen. At Springsure, the only habitat mentioned for *M. Moorei*, the plant is being exterminated so rapidly that in a few years it may be hard to find a specimen. In killing the plant, a notch is chopped in the trunk and a large hole is then bored from the notch to the center of the pith (fig. 12). The hole is filled with arsenic and the plant soon dies. The dead specimens become quite brittle and are soon broken down by the wind. The notch and the characteristic appearance of a poisoned specimen are shown in fig. 12. The species is beautiful and grows rapidly, but it is almost never found in botanical gardens and conservatories. It would be a pity to allow a plant with such good claims to the title of missing link to become extinct, in spite of the fact that it is easily accessible.

Summary

1. *Macrozamia Moorei* bears numerous lateral cones in the axils of leaves, in this respect being identical with the mesozoic Bennettitales.

2. The pollen grain, at the time of shedding, contains a persistent prothallial cell, a generative cell, and a tube cell; the exine does not cover the apical part of the grain. In the young pollen tube the generative cell has given rise to a stalk cell and a body cell like those of other cycads.

3. The archegonial chamber is unusually deep, and the archegonia are of moderate size.

4. The embryogeny resembles that of *Cycas* and differs from that of *Zamia* and *Ceratozamia*.

5. The species, which represents the nearest approach to the mesozoic Bennettitales, is in immediate danger of extinction.

UNIVERSITY OF CHICAGO

A PROTOCORM OF OPHIOGLOSSUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 167

LOREN C. PETRY

(WITH THIRTEEN FIGURES)

Historical

The earliest description of the growing region of *Ophioglossum vulgatum* is by BRAUN (4) in 1839. He recognized the spiral arrangement of the leaves and described the sheathing of the growing point. HOFMEISTER (9) in 1857 described the apical cell of the same species as triangular in transverse section; its exact form was not stated. The vascular cylinder was described as a loose network with a large gap corresponding to each leaf. However, he stated that the bundle connecting with the leaf is sent off from the upper angle of the gap. RUSSOW (13) gave the histological details of the structures of *O. vulgatum*, and pointed out the positions of protoxylem and protophloem.

The first extensive description of the anatomy of this species is by HOLLE (10). He refuted HOFMEISTER's statement that the leaf trace attaches to the upper angle of the gap. He further stated that there is a root corresponding to each leaf and that the bundle of the leaf trace is continuous with that of the root inserted immediately below it. The apical cell is described and figured.

VAN TIEGHEM (14) in 1890 discussed the transition of the vascular cylinder of *O. vulgatum* from a solid stele to the medullated condition, and described an endodermis surrounding each bundle of the mature stem. ROSTOWZEW (12) described the development of young plants of this species from buds upon roots. His figures indicate that the apical cell is sometimes a truncated pyramid.

BOWER (1) in 1896 described the vascular anatomy of *O. Bergianum* as resembling closely that of *O. vulgatum*. He discussed the anatomy of the latter species and decided that the relation between root and leaf is variable. BRUCHMANN (5) described the development of the embryo of this species. The vascular develop-

ment of the sporeling is not given, but it is stated that it follows that of the bud as described by ROSTOWZEW (12).

BOWER (2) in 1904 described the vascular structures of *O. simplex* and *O. pendulum*. In the latter species the many strands of the petiole unite to form 5 bundles which unite separately with the vascular cylinder. CAMPBELL (6) described the usual form of the apical cell of *O. pendulum* as a triangular pyramid; a truncated triangular pryamid was found occasionally. The first division of the segment of the apical cell is transverse. The same author (7, 8) later described the development of the embryo of *O. moluccanum*. The embryo consists of cotyledon and root only; no stem is recognized. The leafy plant arises from a bud upon the root of the embryo.

BOWER (3) in 1911 described the vascular structures of *O. palmatum*, which constitutes the division CHEIROGLOSSA. The stele is a very loose network. The leaf trace is double and the two strands connect with the vascular cylinder at opposite sides of the common gap. Roots are diarch or triarch and sometimes occur within the pith. BOWER concluded that the double leaf trace is a derived condition.

LAND (11) described very briefly a protocorm found in material of *O. vulgatum* from southern Mexico. No details of the structure were given.

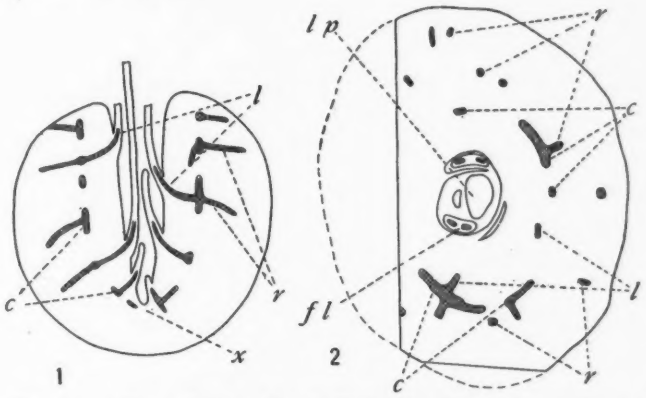
Investigation

The protocorm described by LAND (11) is the subject of this investigation. Its size and general appearance are described in that paper. The specimen was sectioned and examined with especial reference to its vascular anatomy and apical region.

As already stated, the protocorm is approximately spherical and about 9 mm. in diameter. The growing point is at the bottom of a circular pit which extends downward about 0.8 of the diameter of the corm (fig. 1). The functioning leaf arises from this pit and its base is attached to the side of the pit at a distance of about 2 mm. above the growing point. Above the base of the functioning leaf the bases of 6 other leaves are present, and below it the primordia of 6 others occur. The leaves are arranged in an

irregular spiral approximating the $\frac{2}{5}$ arrangement that has been described for this species.

The vascular tissue all occurs *above* the growing point, that is, surrounding the circular pit from which the leaves arise (figs. 1, 2). Each leaf trace consists of two strands which connect separately with the vascular tissues of the corm. The roots extend in a general horizontal direction outward from the vascular tissue; three roots occur between the vascular tissue and the central pit, and run in a downward direction.

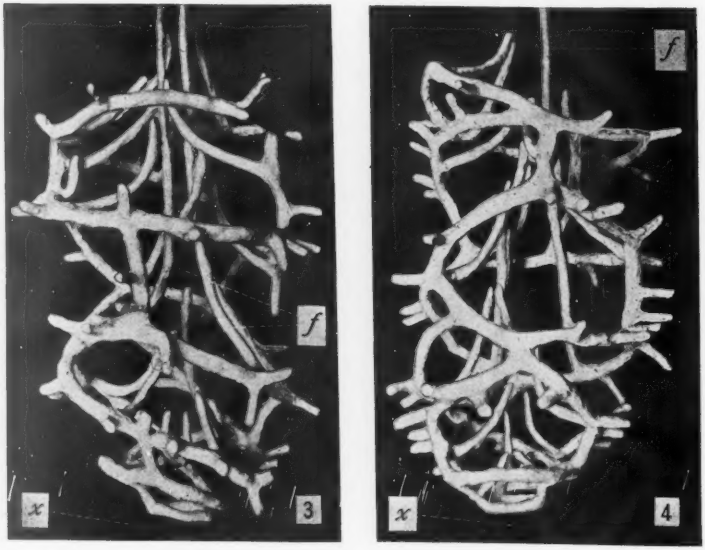


FIGS. 1, 2.—Fig. 1, diagram of longitudinal section through protocorm: *x*, position of apical cell; *c*, cylinder strands; *r*, root strands; *l*, leaf strands; Fig. 2, transverse section of protocorm, 3 mm. above bottom of pit: *lp*, leaf primordium; *fl*, petiole of functioning leaf; *c,c*, cylinder strands; *r,r*, root strands; *l,l*, leaf strands; ×7.

From study of the serial sections a model of the vascular system was built up in clay to a scale of 30 diameters. This was copied in plaster and photographed (figs. 3, 4, 5).

As shown by these figures, the vascular tissue makes up a definite cylinder. Its structure will be understood from the following illustration. Suppose the vascular cylinder of an ordinary rhizome of this species to be turned "wrong side out" by pulling the apical region down through the center of the stele, as one would pull the bottom of an inverted sack through the tubular part. This eversion of the stele of an ordinary rhizome of *O. vulgatum*

would produce a structure differing in only two important particulars from the vascular cylinder of the protocorm: (1) the leaf trace of the inverted cylinder of the rhizome would be a single bundle; the leaf trace of the protocorm consists of two bundles; (2) the roots of the everted cylinder of the rhizome would be within the cylinder; in the protocorm, with three exceptions, they are outside.



FIGS. 3, 4.—Fig. 3, model of the vascular system of the protocorm, from the side: *f*, bundles of the functioning leaf; *x*, position of apical cell; ×8; Fig. 4, model from the side at right angles to fig. 3.

As indicated by this illustration, the oldest portion of the cylinder is at the top of the corm and the formation of new vascular tissue proceeds in a downward direction. There is a gap in the cylinder corresponding to each leaf; no gaps not definitely related to leaves occur. The gap is below the point of attachment of the leaf bundles, as would be the case in the everted cylinder of a rhizome as described above. On either side of a gap a strand runs downward in a nearly vertical direction for a short distance

and then divides into two strands which run almost horizontally and close the leaf gaps on either side. The leaf bundles corresponding to a gap sometimes attach to the vertical strands at the sides of the gap; much more usually, however, they connect with the horizontal strand above the gap, at about 90° apart.

In a single instance, three bundles separate from the strands of the cylinder. Two of these fuse at a very short distance from their points of connection with the cylinder strand, and the two resulting strands form the vascular supply of a leaf.

Along a vertical strand the phloem is upon the inside of the cylinder and the xylem outside (fig. 6). Where the strands run horizontally the phloem is often upon the upper side. This twist of the strands never exceeds 90°, that is, phloem never occurs on the outer side of a strand. The protoxylem is at the outer margin of the xylem area (fig. 7). No endodermis can be distinguished about any of the cylinder strands; both xylem and phloem are bordered directly by unmodified parenchyma.

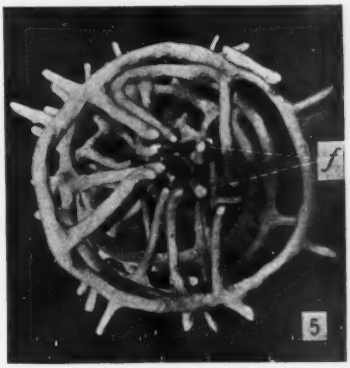


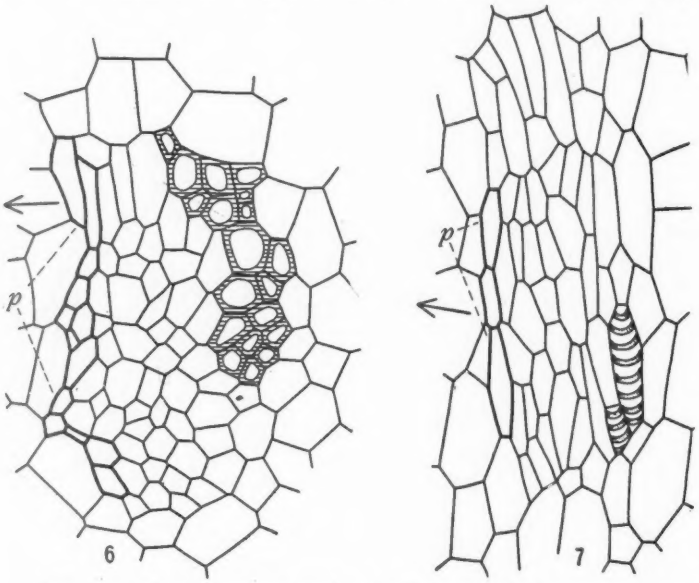
FIG. 5.—Model from above

The leaf bundles, when they separate from the cylinder strands, run horizontally inward for a short distance, then run obliquely upward till they emerge within the central pit. At this point the two bundles of a leaf trace are about 0.5 mm. apart, and they run parallel to each other at this distance through that part of the petiole within the pit.

In the petiole of the leaf the xylem is adaxial, as in an ordinary plant. Where the leaf bundles are horizontal the phloem is above the xylem, and in this position the xylem and phloem connect directly with the corresponding tissues of the horizontal cylinder strands. In the few cases where a leaf strand connects with a vertical cylinder strand, the xylem connects directly. The phloem of the cylinder strand swings to one side to pass the xylem of the

leaf strand and then connects with the phloem upon the upper side of the leaf strand.

The roots grow in a slightly downward direction outward from the vascular cylinder. The root stele is monarch with the phloem above, as described for the roots of this species. Where these attach to a horizontal strand of the cylinder, the xylem and phloem are in the same relative positions in the two strands, and they



FIGS. 6, 7.—Fig. 6, transverse section of cylinder strand of protocorm: arrow indicates direction of central pit; *p*, phloem; ×236; Fig. 7, diagonal section of young cylinder strand of protocorm: arrow indicates direction of central pit; *p*, phloem; ×236.

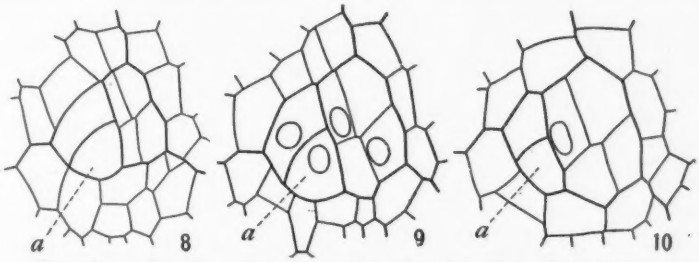
connect directly. Where a root connects with a vertical strand of the cylinder, the xylem of the root connects directly with that of the cylinder strand; the phloem of the root swings to the side of the cylinder strand and passes around to its inner side, where it connects with the phloem of that strand.

The roots are very numerous. There are about sixty-five in which xylem has been differentiated, and probably fifteen more in

which root formation is evidenced by at least an apical cell. A root usually attaches to the cylinder near the point of attachment of a leaf bundle. This produces a cross of vascular tissue, such as is shown in fig. 2. This relation of leaf bundle to root bundle is not invariable.

The ground tissue of the protocorm is a large-celled parenchyma similar to that of an ordinary rhizome. There are no intercellular spaces. The tissue within the vascular cylinder differs in no way from that outside. The cells everywhere are packed with food material, principally starch.

Examination of the sections through the region immediately below the bottom of the central pit of the protocorm shows a



FIGS. 8–10.—Fig. 8, a transverse section of apical region of protocorm, 40 μ below bottom of central pit: *a*, apical cell; ×236; Fig. 9, a section 70 μ below bottom of pit; Fig. 10, a section 95 μ below bottom of pit.

conspicuous apical cell, triangular in cross-section (figs. 7. 8, 9). This apical cell is an inverted triangular pyramid with strongly curved faces. It is about 120 μ in length from vertex to center of base, and each side of the base is approximately 30 μ in length. By reason of the strong curvature of the faces of the pyramid, the cross-section of the cell is greatest about halfway between vertex and base, where each side of a transverse section measures about 42 μ.

The youngest segment of the apical cell has not divided. The next segment has divided twice longitudinally (figs. 8, 9, 10), and one of the resulting cells has divided once transversely, as shown by a count of the nuclei. The outlines of the third segment cannot be traced.

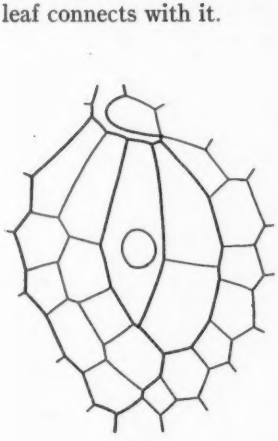
When a segment is first cut off from the apical cell, its principal wall is approximately parallel to that of the apical cell. The lower portion of the segment soon enlarges and the segment assumes the shape of a truncated rectangular pyramid, with the smaller end above. Transverse sections of the second segment, as represented in figs. 8, 9, and 10, show this enlargement of the lower portion of the segment. This unequal growth of the upper and lower parts continues with the further division of the cells of the segment. The result of this unusual manner of growth is represented diagrammatically by fig. 11. As shown by this diagram, the upgrowth of the peripheral region and the resultant everted form of the protocorm are direct results of the behavior of the segments of the apical cell.

FIG. 11.—Diagram showing eversion produced by unequal growth of upper and lower portions of the apical segments.

For purposes of comparison, the apical region of an ordinary rhizome, already described by HOLLE (**10**), was re-examined with especial reference to the divisions of the segments of the apical cell. In all cases examined, the apical cell is a triangular pyramid, as in the protocorm; it measures 120–150 μ in length and 30–50 μ across each face at the point of greatest width (figs. 12, 13). Each segment divides transversely first, that is, by a periclinal wall. Two longitudinal divisions at right angles to each other usually follow in the outer cell of the segment. The inner cell of the segment may divide in the same way, but more usually the divisions are irregular. While the segments cannot be traced to any considerable distance from the apical cell, it is clear that the upper and lower parts of a segment enlarge about equally, in contrast to the unequal growth of the parts of the segment in the protocorm.

Leaves and the sheathing tissue about the leaf bases arise from the upper cell of the segment; stem tissue is produced by the lower cell. Procambium develops very near the apical cell, within the region where the segmentation can be definitely determined (fig. 13). In the case figured, it is certain that the vascular tissue of the stem is being developed directly from segments of the apical cell, and entirely independent of the leaf traces. The

procambium strands figured, when traced through the serial sections, are found to connect. They constitute the vascular strand which closes the gap of the leaf second in order from the apical cell; the procambium of a trace which will supply the youngest leaf connects with it.



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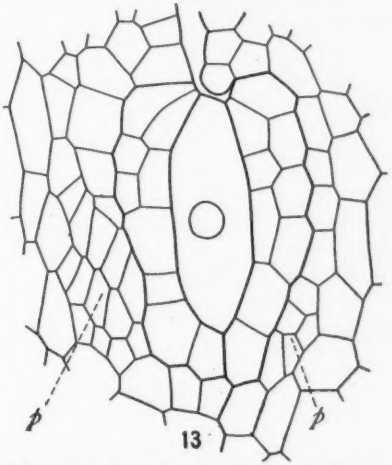

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FIGS. 12, 13.—Fig. 12, longitudinal section through apical region of rhizome; ×236; Fig. 13, longitudinal section through apical region of rhizome: *p*,*p*, procambium strands; ×236.

Discussion

In view of the complex anatomy of the specimen investigated, it seems necessary to state that the term "protocorm" is used by LAND (11) and in this paper without any intended implication that the object so named is necessarily simple in its structure. The name has been applied rather with reference to its external appearance, which is not unlike that of mature plants of *Phylloglossum* and of young plants of *Lycopodium cernuum*, to which the name was first applied.

In order to compare the vascular system of the protocorm with that of an ordinary rhizome of the species, the effects of the unusual behavior of the segments of the apical cell must be taken into account. By reason of the eversion produced, the tissue surrounding the central pit corresponds directly to the cortex of an ordinary rhizome. In the same way, as regards origin, the tissue immedi-

ately outside of the vascular system is pith. The xylem and phloem are therefore, for the most part, placed in the usual collateral arrangement, with phloem next to the cortex. The protoxylem occurs next to the pith. Hence we may describe the vascular system of the corm as an everted ectophloic siphonostele with endarch xylem. The vascular cylinder therefore differs from that of the rhizome only in being everted.

The constant occurrence of a double leaf trace in this specimen is noteworthy. Exactly the same situation has been described for *O. palmatum* by BOWER (**3**). The same writer (**2**) describes the leaf trace of *O. pendulum* as composed of five strands, and thinks it probable that this is the case in all the species of the group OPHIODERMA. If this be true, the specimen described in this paper represents the fifth species of the genus in which a multiple leaf trace occurs.

BOWER points out the fact that those species which have a multiple leaf trace are offshoots of the main line of the genus, and he considers them as derived forms. In the case under discussion, the specimen described belongs to the species usually considered most representative of the genus. It is to be noted that the rhizome of *O. palmatum* is very broad in proportion to its length, and often almost spherical in shape. While the rhizome of *O. pendulum* is relatively small, the figures of *O. simplex* indicate a rather stout stem, and CAMPBELL (**8**) describes the rhizome of *O. intermedium* as "very short, forming a small tuberous body." It seems probable that in the protocorm described above the doubling of the leaf trace is related directly to the extreme lateral expansion of the corm, due to its manner of growth; and it is possible that in the other species of this genus with a multiple leaf trace the same explanation may hold.

If this explanation of the doubled leaf trace is accepted, every unusual feature of the protocorm is definitely related to the peculiar behavior of the segments of the apical cell. It is to be noted that these segments in the protocorm differ in their development from those in the rhizome in two particulars: (1) in the rhizome the first division of a segment is transverse, and the later divisions are variable; in the protocorm the first two divisions are longitudinal;

(2) in the rhizome the upper and lower parts of a segment develop uniformly; in the protocorm the upper and lower parts of a segment grow unequally and the eversion of the corm results.

CAMPBELL (8) states that in *O. moluccanum* there is "no reason for assuming that the tissues of the very open reticulum forming the fibrovascular system of the rhizome is in any part due to additions from the apical tissue of the stem." As pointed out above, this is distinctly not the case in the rhizome of *O. vulgatum*, where the procambium strands are definitely related to the apical cell. It is to be noted also that the procambium of a leaf trace develops first at the point of connection of the strand with the cylinder.

Summary

1. The protocorm is nearly spherical, with a circular pit in the center of the top. This pit extends downward about 0.8 of the diameter of the protocorm, and the apical cell is located at its bottom.

2. The bases of the leaves are attached to the sides of this pit, with the oldest at the top. The functioning leaf is the seventh, and the primordia of six others occur below it.

3. The vascular cylinder is an everted ectophloic siphonostele with endarch xylem. The leaf trace consists of two strands which attach separately to the cylinder. The roots are numerous and outside the cylinder.

4. The apical cell is a triangular pyramid. The segments divide twice longitudinally before a transverse division occurs. The segments enlarge below more rapidly than above, and the eversion of the cylinder results from this.

5. The segments of the apical cell of a rhizome of *O. vulgatum* divide transversely first; the later divisions are irregular. The upper and lower portions of a segment enlarge uniformly.

6. The vascular tissue of the rhizome is produced by the apical cell directly, and is not made up of leaf traces.

The writer is indebted to Professor JOHN M. COULTER for many helpful criticisms, and to Dr. W. J. G. LAND under whose direction the investigation was made. The writer wishes also to express his thanks to Mr. W. A. POYSER for help in securing material.

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CURRENT LITERATURE

BOOK REVIEWS

Soil fertility

RUSSELL[1] has added to the monographs on biological chemistry a volume on soil conditions and plant growth. The table of contents by chapters gives an idea of the scope of the work: (1) historical and introduction, (2) constitution of the soil, (3) carbon and nitrogen cycles of the soil, (4) biological conditions of the soil, (5) soil in relation to plant growth, (6) soil analysis and its interpretation. There is also an appendix on methods of soil analysis. The book contains a bibliography of 323 citations and an index of two pages.

The treatment of the subject deserves characterization as critical, broad, and in the main unbiased. The soil is considered as an environmental factor of the plant, as the title implies, and not merely from the side of chemical and physical analysis. Great emphasis is laid upon the application of BLACKMAN'S idea of limiting factors, a principle the importance of which in biological problems it is hard to overrate. In this connection the author cites data to show that addition of mineral salts has little or no effect on yield if another factor, such as water supply, is already a limiting factor. RUSSELL concludes that soil toxins play no part in the fertility of well cultivated and drained agricultural lands, but admits that they are formed and may remain for some time in poorly drained and "exhausted" land. Some will question whether he has sufficient data for such a sweeping statement in the face of some of the experiments of our Bureau of Soils. Many will commend the caution with which he uses the term "available nutrients," or in his terminology "available food," also his lack of readiness to distinguish sharply between "essential" mineral salts and other salts and even organic compounds that increase yield.

In spite of the breadth of treatment that characterizes the monograph in the main, and the evident attempt of the author to give every soil factor affecting growth and yield its proper emphasis, it is evident that he turns more often than our present knowledge will insure to deficiencies of some mineral nutrient as the limiting factor. For instance, he attributes increased yields due to heating soils or treating them with poisons to the increase in ammonium salts due to differential killing of soil organisms, thus furnishing a greater nitrogen supply. It is true that there is some questionable evidence

[1] RUSSELL, EDWARD J. (Rothamsted Experimental Farm), Soil conditions and plant growth. viii+168. London: Longmans, Green & Co. 1912.

that such treatment leads to an increase in ammonium salts, but it is not shown that such an increase of ammonium salts, by furnishing more nitrogen, will cause such a rise in yield, nor that the beneficial effects are not due to any one of half a dozen other possible changes in the soil. BOLLEY has some evidence that in the wheat lands of North Dakota such treatment increases yield by killing certain parasitic fungi.

Since SCHREINER and his collaborators have shown that many organic substances, some toxic and some stimulative to higher plants, are produced by decomposition of the organic débris of the soil, it is possible that the effect here is due to accumulated organic substances of one sort or another brought about by unbalancing the soil flora or fauna. Our Bureau of Soils has also collected much other data showing the extreme complexity of the problem of fertility and the danger of reasoning too directly from the mineral nutrient theory.

There are a number of minor defects involving form of statement, degree of emphasis, and errors of fact (certain to creep into the most carefully written book) that deserve notice. Only a few of these can be mentioned. Considering the idea RUSSELL wishes to convey, it seems better to use the more specific term "mineral nutrient" than the word "food." The author considers that non-available water is such because of the concentration (osmotic activity) of the salts in it (p. 104). Known facts in this matter indicate clearly that the resistance to absorption is capillary. Rendering soil toxins innocuous by oxygenating or by filtering over fine powders is described as precipitating them (p. 133), whereas the process in the first case is oxidation and in the second adsorption. No mention is made of the importance of surface tension in soil phenomena, though it plays an important rôle in flocculation, deflocculation, localization of solutes, etc.—WILLIAM CROCKER.

The evolution of plants

This little volume by SCOTT[2] belongs to a not unfamiliar category, but it is rare to find a work on evolution written by an eminent morphologist and a distinguished paleobotanist. This constitutes such an unusual equipment that although the work under consideration is popular in its appeal, the mode of treatment is of interest to the professional botanist.

The author at the outset draws a happy parallel between the value of our knowledge of fossil forms as a key to the course of plant evolution in general and the history of cultivated varieties of plants in relation to their derivation from wild ancestors. In a second chapter the characteristics and statistics of the angiosperms are dealt with, special emphasis being laid on the external organization of the angiospermous flower. In the third chapter the gymno-

[2] SCOTT, D. H., The evolution of plants. pp. 256. *figs. 25*. New York: Henry Holt & Co. 1912. 75 cents.

sperms are discussed, which as the author points out constituted the characteristic vegetation of the secondary or Mesozoic period, just as the angiosperms are of the present. Here, in accordance with the author's well known point of view, the Cycadophytes receive a very large amount of attention, to the practical exclusion of the actually as well as mesozoically much more important Coniferales.

Beginning with the living cycads, which are remarkably well summarized as to their characteristics and distribution, SCOTT continues with a description of the more important features of the mesozoic Cycadophytes, the Bennettitales. These are elaborated chiefly in connection with the hypothesis revived in recent years by WIELAND, that they are the direct ancestors of the angiosperms. Here the distinguished author, so well known for his anatomical investigations, pins his faith unreservedly to the externals of their reproductive structures. His summary of their angiospermous features is as follows: (1) the presence of flowers organized on the same general plan as the typical flowers of the angiosperms; (2) the formation of a fruit inclosing the seed; (3) the exalbuminous character of the seed. SCOTT concludes in regard to the Bennettitales and their supposed angiospermous affinities: "They have thus proved to fully deserve the name Proangiosperms, which SAPORTA, by a brilliant inspiration, gave to *Williamsonia* and *Bennettites*, at a time when their stucture was very imperfectly known." It is perhaps worth while to recall in this connection that ASA GRAY, who knew his Compositae perhaps better than any other person living, referred the genus *Williamsonia* with conviction to the Compositae. Apparently the reproductive structures of the Bennettitales may be quite as appropriately regarded as equivalent to the inflorescence of this high group of dicotyledons as that of the flower of the lower angiosperms. Surely here Homer nods!

One of the most interesting chapters is that in which the author deals with the fernlike seed plants, which he himself has done so much to rescue from oblivion and restore. With characteristic modesty he makes no reference to his own contributions in this interesting field. The Medulloseae are apparently now regarded as more nearly allied to the cycad stock than the Lyginodendreae, thus slowly reversing the opposite conclusion adopted by the author in earlier years.

The book concludes with chapters on the true ferns, the club mosses, and horsetails (together with sphenophylls), which latter SCOTT still prefers to associate with the fern stock. The closing remarks on the relation of the paleobotanical record to the general principles of plant evolution are of particular value, most of all the statement as to evolutionary progress being more frequently from the more to the less complex and not vice versa, as is too often assumed by writers on evolution. Would that SCOTT and other English morphologists might focus their attention on this principle in dealing with anatomical structures!—E. C. JEFFREY.

The natural history of coal

There is perhaps no substance of vegetable origin of greater importance and intellectual interest than coal. Nevertheless, we are largely ignorant of its composition and mode of formation. What knowledge we possess is almost exclusively based on inferences drawn from the organization of the rocks lying above and below the actual coal beds. Obviously inferences derived from such data are as open to error as the judging of the character of a book from the nature of its bindings. The geologists have notably failed to give us any adequate description or explanation of this greatest of mineral products, and it is now obvious that we must look to the anatomist and the paleobotanist, in collaboration with the chemist and physicist, to clear up this literally as well as figuratively dark subject.

ARBER[3] has stated the problem in an admirably clear and succint way, and has interestingly summed up the history of our knowledge of coal to the present time, with indications of the probable lines of successful attack in the future. It is noteworthy that the greatest recent modifications of our views in regard to coal have come about from the successful preparation of microscopic sections of certain types by the French investigators BERTRAND and RENAULT. It is now realized that a considerable number of combustible minerals have been formed in open water, and are to a large degree composed of the remains of phytoplankton (autocthonous and allocthonous). This is notably the case with coals rich in gases and hydrocarbons, such as cannels, bogheads, oil shales, bituminous shales, etc. Our information in regard to the coals which are not bituminous, or at least not markedly so, is in a less advanced state on account of the impossibility until quite recently of securing sections of the coal substance sufficiently thin and decolored to show their organization. On this subject ARBER writes as follows: "If we prepare thin slices of coal, ... and examine them under the microscope, we shall find as a rule that they are very disappointing as regards the amount of information we can obtain from them. Such sections are usually opaque, even when quite thin, and the substance is obviously very homogeneous." Fortunately the difficulties here described have quite recently been almost entirely obviated, for it has been found possible to prepare fairly thin and translucent sections even by the grinding method used by the petrographer, and by a modified biological technique it becomes feasible to prepare transparent slices of practically all categories of coals.

The writer shows that the old chemico-physical hypothesis of the origin of the various categories of coal, the peat-to-anthracite theory, is no longer tenable, but must be replaced as our knowledge permits by biological and biochemical hypotheses. The nature of a coal, where we are at present acquainted with its real composition, depends as much as anything on the

[3] ARBER, E. A. NEWELL, The natural history of coal. Cambridge Manuals of Science and Literature. pp. 163. *figs. 21.* Cambridge University Press. 1911. 1s.

character of the plant remains which compose it, and to a much less degree on the chemical and physical conditions to which it has subsequently been exposed. It is accordingly clear that the study of coal is to a very large extent within the domain of the biologist, for certainly no adequate conception of the problem can be reached without his cooperation.

There are a few slips on the part of the author; for example he states that anthracite and cannel differ from ordinary so-called bituminous coal and oil shale or boghead respectively, by the fact that they contain little or no ash. Obviously this statement does not generally hold of these types of coal as mined in North America. ARBER has confined his observations in this respect to European coals. His book is nevertheless planned on the broadest lines, and is commended to all who wish to obtain a clear conception of our present knowledge of coal.—E. C. JEFFREY.

NOTES FOR STUDENTS

Recent work in gymnosperms.—In 1910 SCOTT and MASLEN established the genus *Mesoxylon* to include certain paleozoic stems intermediate in structure between *Poroxylon* and *Cordaites*, giving diagnoses of five species. One of these (*M. Sutcliffii*) has been described in detail by MASLEN,[4] and now two more species are described by SCOTT.[5] The conclusion is reached that *Mesoxylon* is "the last link in the chain of fossil types connecting the Pteridosperms with the typical *Cordaites* of the Upper Paleozoic," being definitely distinguished from it only by the presence of centripetal xylem in the stem. A critical discussion of the relationships of the new genera recently established by ZALESSKY is also given.

Mrs. THODAY and Miss BERRIDGE[6] have made an anatomical investigation of the strobili of four species of *Ephedra* (*E. altissima*, *E. distachya*, *E. fragilis*, *E. nebrodensis*). The "clearly bifid" stamen of the three last named species, each half bearing four bilocular synangia, is traced into other species in which the bifid character is not evident, but in which there are fusions of synangia into trilocular or even quadrilocular synangia, until *E. altissima* is reached with only two bilocular synangia. A reduction series is also traced from the staminate disk of *Cycadeoidea*, through other disks of Bennettitales, to *Ephedra*, where the disk is reduced to two segments, each bearing two pairs of bilocular synangia, and to *Welwitschia*, with its disk of six segments bearing trilocular synangia. It is also discovered that the solitary ovule of the species investigated is the product of a fusion of the two ovules of the biovulate species, since

[4] Rev. in BOT. GAZ. **52**:326. 1911.

[5] SCOTT, D. H., The structure of *Mesoxylon Lomaxii* and *M. poroxyloides*. Ann. Botany **26**:1011–1030. *pls. 87–90.* 1912.

[6] THODAY (SYKES), MARY G., and BERRIDGE, EMILY M., The anatomy and morphology of the inflorescences and flowers of *Ephedra*. Ann. Botany **26**:953–985. *figs. 21. pl. 85.* 1912.

E. altissima revealed a long series of intermediate forms. This suggests that the solitary ovule of *Ephedra* and of *Welwitschia* represents a fusion of "the many ovules and interseminal scales of such a flower as *Cycadeoidea*."

THOMPSON[7] has attacked the problem of the affinities of the Gnetales with the anatomical weapons forged in the study of the conifers and the primitive dicotyledons. In this first paper the genus *Ephedra* is considered, the anatomical features being described in detail. The idea that *Ephedra* may be connected with the Bennettitales or the Cycadales receives no support from the anatomy; on the contrary, the suggestions of relationship to the Coniferales are numerous (arrangement of primary vascular bundles, double leaf trace, arrangement and structure of the tracheid pits, bars of Sanio, tertiary spirals, trabeculae and resin plates, primitive uniseriate lignified rays, wood parenchyma, and endarch leaf bundles). It is further evident that the group could not have arisen from any of the modern conifers, but rather "from or close to the base of the coniferous line." An angiospermous affinity is indicated clearly "by the possession of true vessels, broad rays, formation of broad rays by fusion, and separation of the leaf traces." These general conclusions are abundantly confirmed by the morphological evidence.

Miss BERRIDGE[8] has discovered that a ring of complex groups of vascular strands arises from the bundles in the base of the ovulate "flower" of *Gnetum Gnemon*, and suggests that this may indicate that the ovule was "primitively surrounded by a whorl of male flowers." This would mean that the ovulate strobilus of *Gnetum* was originally bisporangiate.—J. M. C.

Evolution of araucarians.—Probably the most discussed question in connection with the phylogeny of conifers is the relationship of the araucarians to the Abietineae. So far as the historical evidence goes, the two tribes are rivals in age, and the araucarians seem to have been the dominant coniferous vegetation during the Mesozoic. The complete separation of araucarians from Abietineae, by suggesting either their direct origin from the Cordaitales or even from club-mosses, is an idea that has entered into the discussion.

JEFFREY has been a staunch defender of the primitive character of the Abietineae, and of the derivation of the araucarian type from this stock. In a paper just published,[9] he attacks the problem of the evolution of the araucarian type on the basis of a study of abundant material of the existing forms, which is compared critically with the mesozoic material. So far as the evidence of history and anatomy goes, the whole series, from the abietineous stock to

[7] THOMPSON, W. P., The anatomy and relationships of the Gnetales. I. The genus *Ephedra*. Ann. Botany **26**:1077–1104. *figs. 2. pls. 94–97.* 1912.

[8] BERRIDGE, EMILY M., The structure of the female strobilus in *Gnetum Gnemon*. Ann. Botany **26**:987–992. *figs. 4.* 1912.

[9] JEFFREY, E. C., The history, comparative anatomy, and evolution of the *Araucarioxylon* type. Proc. Amer. Acad. **48**:531–571. *pls. 7.* 1912.

the living araucarians, becomes evident. Throughout the investigation it is assumed that the appearance of a character in response to wounding means the recall of an ancestral character.

The combination of characters that makes the araucarian wood unique among living conifers is the close-set and alternating pits of the tracheids, the absence of the bars of Sanio, the usual absence of wood parenchyma, and the much restricted pitting of the ray cells. The wound reactions obtained from living araucarians, combined with the structure and wound reactions of mesozoic forms, lead to the conclusions that the ancestors of the existing araucarians were characterized by the presence of wood parenchyma and by strongly pitted rays. Both of these features are inconsistent with direct derivation from the Cordaitales. The living araucarians have retained in the cone axis, root, and first annual ring of vigorous branches, the characteristic features of the mesozoic forms. It is further shown that the characteristic pitting of the tracheids of *Araucaria* and *Agathis* is not ancestral, but acquired. A very significant result is that obtained from a study of the resin canals, which shows that certain mesozoic araucarians possessed traumatic resin canals; and even in a living *Agathis* normal resin canals were found in certain peripheral regions.

The general conclusion is reached that the araucarians are not derived from the Cordaitales, since their primitive forms possess a number of features that have not been discovered among the Cordaitales. The araucarian type is derived from ancestors with opposite (not alternate) pitting, bars of Sanio, strongly pitted rays, and horizontal and vertical resin canals. This group of ancestral characters selects *Pityoxylon* as the ancestral abietineous type. There seem to be no question that the araucarian and abietineous stocks blend characters in the Mesozoic, and that recognizable araucarians started with numerous abietineous characters that gradually disappeared, until the existing araucarians are very distinct.—J. M. C.

Induction of inheritable changes in plants by ovarial injections.—FIRTH[10], in an apparently preliminary paper, has given the results of experiments, carried on in the hills of India, wherein it was attempted to produce "mutations" by the injections of different salts into the ovaries of plants, and also by the use of external conditions in the medium, and the adding of salts to the soil water. Pure cultures of *Oenothera Lamarckiana*, *O. tetraptera*, *O. odorata*, *Epilobium parviflorum*, *E. cylindricum*, and *E. hirsutum* had been kept in the garden and grown in "pure pedigreed strains" from 1906 to 1908. These were subjected to different experimental conditions of light relations, temperature relations, soil relations, and the injection of salts into the ovaries. Positive results seem to have been obtained in *E. parviflorum* when watered

[10] FIRTH, R. H., An elementary inquiry as to the origin of species. Jour. Royal Army Medical Corps **16**:497–504. 1911.

with solutions of nitrate of potassium, in one series, which gave seeds, from which plants were grown "in which the stem and leaves were marked by very shaggy hairs, the leaves were definitely stalked, not sessile, distinctly stem-clasping, in shape ovate, with large sharp teeth." The new form, which did not conform to any known type, was carried "successfully" to the second generation but not beyond. These experiments were repeated in 1909–1910 but gave negative results.

Injection of salts into the ovary before fertilization, in dilutions of 1:1000, showed many failures by killing the "unfertilized ovules." Sodium chloride, nitrate of potassium, carbonate of ammonium, sulphate of sodium, and sulphate of iron were used. One series in which sodium chloride and carbonate of ammonium were injected into the ovaries of *E. roseum* showed "a number of aberrant forms of quite unknown type." "Three of the new forms were brought to bloom and maturity, and in one case to a second generation."

O. Lamarckiana when injected did not show any increased array of new types, but *O. odorata*, after the injection of carbonate of ammonia, produced a "bloom" "which reminded one strongly of *O. gigas*." It was sterile. In *E. hirsutum* only injections of nitrate of potassium gave results, and in one series there resulted a form that had many of the "features of another genus, namely *Circaea*," which reverted to the type of the parents in subsequent generations.

Apparently the paper is a preliminary announcement, and one regrets that it is not accompanied by illustrations and more data of the experiments and less of the general discussion of the problems. The chief interest in the paper lies in the fact that FIRTH apparently did not know of MACDOUGAL's investigations along the same line, nor of the experiments of HUMBERT upon *Silene noctiflora*. FIRTH used the same methods that have been used by MACDOUGAL, but somewhat stronger solutions, and his results are an important confirmation of the general results obtained and methods employed by MACDOUGAL.—W. L. TOWER.

Effect of neutral salts upon plants and animals.—OSCAR LOEW[11] has investigated the effects of neutral salts upon the lower animals and plants. He finds that a 0.2 per cent solution of di-potassium oxalate more poisonous to infusoria than a 1 per cent solution of di-potassium tartrate. Infusoria, copepods, and rotatoria, which are able to live 24 hours (and some 3 days) in a 0.5 per cent di-potassium tartrate, die in 30–40 minutes in a 0.5 per cent solution of di-potassium oxalate. Seedlings of radish, clover, and barley, with root length of 1–3 cm., exposed to 0.5 per cent of the oxalate at a temperature of 12°–15° C., show loss of turgor in the root cells within 24 hours, and decay immediately follows, while in an equimolecular solution of the tartrate or a

[11] LOEW, OSCAR, Über die Giftwirkung von Oxalsaurensalzen und die physiologische Funktion des Calcium. Biochem. Zeitschrift **38**: 226–243. 1912.

0.5 per cent solution of sodium nitrate, they suffer little or no injury. Pea seedlings die in 2 days in a 0.5 per cent of sodium oxalate, but are still uninjured in an equally strong solution of sodium acetate.

In *Spirogyra* the first structure to show the effect is the nucleus, which contracts and becomes lens-shaped. A little later the chloroplasts begin to contract. LOEW finds that the effect is not due to acidity, since 0.005 per cent of oxalic acid is more injurious than 0.01 per cent of citric acid, and 0.0001 per cent more injurious than 0.001 per cent of tartaric acid.

LOEW concludes that the injurious effect of the oxalates is due to the extraction of calcium from the nucleoproteins, chromatin, and plastin, and its replacement by potassium or some other element, and their bringing about a change in the imbibing power of the different parts of the protoplasm. He thinks that calcium is an essential element in the cells of the higher animals and plants.—J. N. MARTIN.

Sutcliffia.—Miss DE FRAINE[12] has made a painstaking investigation, by means of the well known wax plate method of modelling, of the vascular system of *Sutcliffia*, a new genus of the Medulloseae established by SCOTT. Unfortunately the specimen is rather badly dilapidated and for that reason a certain reserve is necessary in interpretation. The vascular system as described by Miss DE FRAINE consists of a large axial "protostele" (sic!) surrounded by three more or less clearly identifiable "meristeles." In addition to these are a number of "extrafascicular" bundles. By a process of reasoning which it is difficult to follow, the author identifies the central "protostele" with the ring of bundles in the Cycadales. It would seem to be in accordance with the general principles of vascular anatomy to regard it as a medullary bundle, and the three surrounding strands as corresponding to the cylinder system of bundles, a conclusion rendered extremely probable by the fact that it is with these that the leaf traces become continuous. *Sutcliffia* is considered to be a primitive type regardless of the fact that it has an extremely multifascicular foliar supply. This would appear to be entirely against all established principles of anatomy. It is gratifying to find that English authors are gradually coming around to the standpoint in regard to the affinities of the Cycadales, namely as rather with the Medulloseae than the Lyginodendreae, which has been held in continental Europe and this country for more than a decade.—E. C. JEFFREY.

Cause of leaf fall.—In a limited series of experiments conducted with detached twigs of various deciduous trees placed in water in a saturated atmosphere, VARGA[13] has attempted to establish the relationship between this

[12] DE FRAINE, E., On the structure and affinities of *Sutcliffia*, in the light of a newly discovered specimen. Ann. Botany **26**:1031–1066. *figs. 19. pls. 91, 92.* 1912.

[13] VARGA, OSKAR, Beiträge zur Kenntnis der Beziehungen des Lichtes und Temperatur zum Laubfall. Oesterr. Bot. Zeitschr. **61**:74–88. 1911.

phenomenon and the processes of transpiration and photosynthesis influenced by various conditions of light and temperature. These experiments seem to show that (1) any decided checking of photosynthesis either from light conditions or from a deficiency of carbon dioxide brings about leaf fall; (2) any lowering of transpiration also produces defoliation, but less rapidly than decreased photosynthesis; (3) variation in the intensity and quality of the light has no direct specific action upon leaf fall; and (4) lower temperatures are efficient in causing leaf fall through decreased photosynthesis and transpiration only within limits which permit the activities involved in the development of the absciss layer; below these limits the leaves die, but cling rather persistently to the twigs. It is to be regretted that the experiments were so limited and hence so few data were accumulated in support of the conclusions reached.—GEO. D. FULLER.

The Forest Club Annual.—Among the publications which tend to promote an intelligent interest in the problems of forestry this annual[14] from the University of Nebraska is worthy of something more than passing notice. Among the articles it contains are "Grazing investigations on our national forests," by A. W. SAMPSON, and "Effects of forests upon run-off in the Rockies," by R. D. GARVER. Both present data that are important from the ecological as well as the economic point of view. The same may be said of "Notes on winter-killing of forest trees," by C. P. HARTLEY, which shows the need of careful investigation of the various physical factors involved before any adequate explanation of the action of winter conditions upon forest trees may be obtained. The other problems discussed include forest conditions in parts of Nebraska and Arkansas, forest roads, trees suitable for streets and parks, and some phases of lumber manufacture.—GEO. D. FULLER.

Fairy ring fungi.—These well known fungi are found by BAYLISS[15] to be parasitic upon the roots of grass. They soon kill the roots by the secretion of some toxic substance. The same or some other secretion is toxic to the fungi themselves, making them unable to grow in the same soil for three years in succession and hence producing the well known development of yearly widening rings. Contrasted with the infected grass, that which lies immediately outside as well as inside the ring is stimulated into better growth by the greater abundance of nitrogenous food made available by the action of the mycelium of the fungi in secreting proteolytic enzymes. The yearly increase in the radii of the rings of *Marasmius oreades* was found to be 6–14 inches. —GEO. D. FULLER.

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[14] The forest club annual, vol. 4, pp. 160. University of Nebraska, Lincoln, Neb. 1912.

[15] BAYLISS, JESSIE S., Observations on *Marasmius oreades* and *Clitocybe gigantea* as parasitic fungi. Jour. Econ. Biol. 6: 111–132. 1911.

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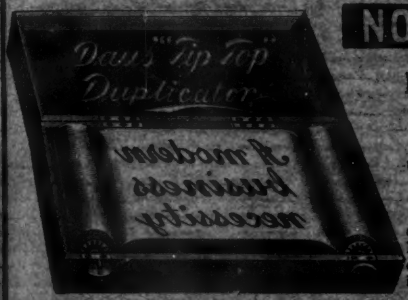

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